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BULLETIN OF THE GEOLOGICAL SOCIETY OF AMERICA
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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

1. INTRODUCTION

By Richard Foster Flint

"When the work of the geologist is finished and his final comprehensive report written, the longest and most important chapter will be upon the latest and shortest of the geologic periods. The chapter will be longest because the exceptional fullness of the record of the latest period will enable him to set forth most completely its complex history. The changes of each period—its erosion, its sedimentation, and its metamorphism—obliterate part of the records of its predecessor and of all earlier periods, so that the order of our knowledge of them must continue to be, as it now is, the inverse order of their antiquity.

"The great importance of the chapter on the latest period lies in the fact that it will contain the key for the decipherment of the records of the earlier.... It is through the study of the phenomena of the latest period that the connection between present processes of change and the products of past changes is established."

Thus did G. K. Gilbert (1890) open his classic treatise on Lake Bonneville. The importance of Pleistocene study has never been better stated, but the statement is inadequate in one important respect. It presents only the point of view of the geologist. Research since Gilbert's day has made it clear that a full understanding of the last million years or more of geologic history cannot be attained without co-operative research in many fields, of which geology is only one, albeit perhaps the most important one in that it provides the frame-work into which the results in other fields are fitted.

Paleoanthropology and archaeology are concerned with early man—apparently a strictly Pleistocene animal—and his industry. Botany and Zoology are concerned with the various geographic assemblages of plants and animals that have preceded the present ones; their fields merge with those of the paleobotanist and the paleontologist. Climatology is concerned with the character and succession of climates in Pleistocene as well as earlier times. Geomorphology interprets the origin of land forms, a large proportion of which are Pleistocene. From soils pedology draws inferences as to the geographic conditions under which they were formed. Glaciology deals with the genesis and properties of the various kinds of ice that played an important part in Pleistocene world history. Geography is interested in various aspects of these problems.

Within the field of geology itself, Pleistocene research does not constitute a distinct entity. It is parceled out within nearly all the departments of geologic study, notably glacial geology, stratigraphy, sedimentology, geomorphology, paleontology, and the newly arrived department of sea-floor geology. Only one of these departments, glacial geology, is specifically oriented toward the Pleistocene. In most of the others, Pleistocene study is hardly more than an incidental part of the whole range of its interests.

At least two serious practical difficulties hamper co-ordination and free lateral communication among the research workers in these fields. One is the departmentalization of universities, museums, and government research institutions, which creates invisible but effective bulkheads between workers and restricts the allocation of research funds outside the conventional, well-established channels. The other difficulty, just as serious, is that means of publication, likewise, are departmentalized, so that it is impossible for a research worker interested in the whole field of the Pleistocene to read the current literature in the field as a whole, or even to be aware of the existence of all of it.

Hence, the student of almost any phase of

the Pleistocene is working at least partly in the dark. He is deprived of many of the available data within the whole field, and therefore he is deprived of keys that would unlock some of the closed doors along his own special research corridor. Yet in no other division of earth history is research intercommunication among many sciences as necessary as in research on the Pleistocene.

As a start toward correcting this situation—toward creating lateral communication through these invisible organizational bulkheads that interfere with research progress—the Committee on Interrelations of Pleistocene Research was created. Set up by the Division of Geology and Geography of the National Research Council in June 1947, this committee includes representatives of most of the fields of interest in the Pleistocene. The members of this group, charged with attempting to furnish the needed lateral coordination, and their fields of responsibility, are as follows:

Henri Bader, Bureau of Mineral Research, Rutgers University (glaciology); Edward S. Deevey, Jr., Department of Biology, Yale University (biogeography); Loren C. Eiseley, Department of Anthropology, University of Pennsylvania (anthropology and new-world archaeology); Richard Foster Flint, Department of Geology, Yale University, chairman of the Committee; Claude W. Hibbard, Museum of Paleontology, University of Michigan (vertebrate paleontology); Chauncey D. Holmes, Department of Geology, University of Missouri (glacial erosion and sedimentation); Helmut E. Landsberg, Committee on Geophysics and Geography, Research and Development Board, Washington, D. C. (meteorology and climatology); Hallam L. Movius, Jr., Peabody Museum of Archaeology and Ethnology, Harvard University (old-world archaeology); Fred B Phleger, The Woods Hole Oceanographic Institution (oceanography and seafloor geology); Louis L. Ray, U. S. Geological Survey, Washington, D. C. (glacial stratigraphy; alpine glacial geology); H. T. U. Smith, Department of Geology, University of Kansas (Eolian features; frozen ground; stream terraces); and James Thorp Division of Soil Survey, U. S. Department of Agriculture, Lincoln, Nebraska (soil science).

The whole Committee has met twice for long discussions, and between the meetings a great bulk of correspondence has passed among the members. Unanimously the group conceived its first task to be one of stock-taking—that is, to assemble the significant information we have and to make it generally available, together with outstanding references to the literature. The result is a symposium, to which the present paper is an introduction. The symposium constitutes a First Report to the Division of Geology and Geography, National Research Council.

The ultimate aim of the Committee is the highest possible synthesis of Pleistocene history, as nearly complete a historical reconstruction as can be made. That aim is for the future; the present symposium is no more than a first step toward it.

There is no single key to the ultimate synthesis. That can be achieved only through skilled and patient research in every pertinent field. Yet certain departments of research are especially significant because we think they may furnish keys to several locked doors.

One is research into methods of determining absolute age—the age in years—of important stratigraphic horizons. Research in this field is important not only inherently but because reasonably accurate absolute-age determinations would aid enormously in correlating physically discontinuous stratigraphic units, and would throw light on such problems as rates of organic evolution and the antiquity of man. Progress in this field was reviewed by the writer (Flint, 1947, p. 379–406). The most promising line of attack seems to be that of study of radioactive elements. This is emphasized by Urry (1949). It is also dramatically underlined by the work in progress on radioactive Carbon 14 (Libby, Anderson, and Arnold, 1949). If the absolute date of the maximum of the Mankato Glacial subage can be determined by this method, then, from it, rough dates can be obtained for several much earlier times. This is because existing time estimates for the four glacial-age maxima, based on degree of chemical decomposition of the drift sheets, are calculated from a wholly arbitrary assumption as to the date of the Mankato. (*See* Flint, 1947, p. 392–402.)

A second field of research of specially wide

significance is stratigraphic correlation in the broad sense. This field is included in several of the contributions to the present symposium, among them physical stratigraphy, paleontology, biogeography, climatology, and the interpretation of stream terraces. Here correlation is far more difficult than among pre-Pleistocene stratigraphic units, because in the Pleistocene we have many more kinds of information to integrate into a single chart. Climatic fluctuations play a part in Pleistocene correlation that is matched in no other bracket of the geologic column. This is one reason why Pleistocene stratigraphic correlation is not yet far advanced, and is the main reason why the world has not yet produced an overall Pleistocene stratigrapher.

Another factor in the poor state of the present correlation chart, especially in Europe, is the wide and erroneous use that has been made of archaeologic data in stratigraphic correlation. In his contribution to this symposium, H. L. Movius has stated the far-reaching opinion that the taxonomic laws that govern the natural sciences do not apply to prehistoric archaeology, inasmuch as artifacts are not natural phenomena but rather are social documents; hence artifacts cannot be used as a basis of stratigraphic correlation, except very broadly. The importance of this opinion can hardly be overemphasized.

Another source of error in stratigraphic correlation hitherto has been the incautious use of stream terraces, which are full of pitfalls for the too-enthusiastic, unwary worker. Some of these pitfalls are set forth in the contribution by H. T. U. Smith.

Probably the standard Pleistocene stratigraphic section will come to be represented by the sequence of sediments on the sea floor, where there has been great continuity of sedimentation both areally and in time, and where the great destroyer, erosion, has been at a minimum. The potent possibilities in this field are outlined in the contribution of Fred B Phleger, Jr.

A third field of outstanding importance is the mapping and interpretation of emerged Pleistocene marine strand lines, which exist in many coastal regions but about which little is known. Not only are strand lines directly important for stratigraphic correlation, but also their correct interpretation will throw much light upon former fluctuations of sea level, especially during interglacial ages.

No member of the Committee pretends that this symposium is complete. Ideally, additional fields should be represented in it. One is invertebrate paleontology; another is the pluvial-lake records of regions dry under today's climates. Still another is the crustal movements during the Pleistocene, whether generated by glacial loading or by nonglacial causes. These and other fields are not represented for a variety of wholly practical reasons, but not because they are not thought important and not because the Commiteee has failed to consider them.

Although each contribution has been critically read twice by every other member of the Committee, it represents essentially the individual opinion of its author, as a specialist in his own field, tempered by discussion with the whole group. The lengths of the papers vary widely. The variation is a result of the greatly varying bulk of the literature in the various fields, of the time elapsed since the time of publication of the latest previous general synthesis or review (if any) in each field, and of the time each contributor had available to devote to his allotted task. Special mention should be made here of the contibutions of E. S. Deevey in the field of biogeography; these constitute nearly half the length of the symposium. This field is represented by no previous synthesis and involves peculiarly great and intricate detail. Hence Doctor Deevey's papers will be widely recognized as having special importance. Workers in each field represented in the symposium will recognize in the other contributions not only syntheses but also original material of great worth.

The National Research Council generously appropriated $500.00 for the purchase of separate copies of the symposium, to be sent free of charge to scientists in countries whose currency-exchange regulations would prevent private purchase. Transportation of the separates to foreign destinations was kindly undertaken by the Smithsonian Institution. Individual contributors, of course, obtained separates of their own contributions for private distribution.

Both Dr. D. W. Bronk, Chairman of the National Research Council, and Dr. Arthur Beven, Chairman of its Division of Geology and Geography, have been thanked by the Committee for their encouragement of its efforts and for financial support of the Committee's meetings.

It is the hope of the Committee that this symposium will cross the traditional barriers and reach every scientist to whom it could have value, wherever he may be, and that, within one or another of the papers, many workers will find something that will enhance the scope or the significance of their own research effort.

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Yale University, New Haven, Conn.
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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

2. TRENDS IN GLACIOLOGY IN EUROPE

By Henri Bader

There have been two fairly distinct phases of development in glaciology—the early era ending approximately at the turn of the century, and the succeeding one ending in the late 1930's.

The early era is by far the more inspiring, filled with exciting discovery and vigorous polemics. A dozen men of caliber, such as Agassiz, Heim, and Tyndall, compiled volumes of observation and speculation. These classical naturalists of the middle nineteenth century were not shackled by specialization. They freely crossed lines which have grown into barriers to the modern specialist, for natural science was then only beginning to really divide into separate faculties. The universalism of approach to early glaciology was its most valuable feature, and remains a source of inspiration.

The rapid specialization of scientists near the turn of the century was disastrous to glaciology. It was classified as a geological science, and from then on glaciers were studied very largely by geologists, with the emphasis on glacial geology. Petrographers and mineralogists generally failed to consider snow and ice as sedimentary and metamorphic rocks and paid them little attention. Physicists were not particularly attracted to the study of a material requiring a refrigerated laboratory, and contented themselves with routine measurements of the more common physical properties of ice. Chemists and biologists saw little to be gained in the study of practically pure and sterile ice. And finally the remoteness of glaciers from centers of industry and main lines of communication effectively prevented them from becoming an object of engineering research.

So, for decades, glaciers belonged to explorers, mountaineers, and geologists. They were objects to be discovered, feared and admired, and studied geologically. As a result we know where the world's glaciers are, what they look like, the dangers they threaten, and the morphological and geological consequences of their presence.

Geologists have given us splendid records of the gross aspect of glaciers, such as advance and retreat, erosion and deposition, surficial motion and surface morphology, accumulation and ablation. One reward of this effort is Pleistocene glacial geology. But these records apparently do not offer a key to a satisfactory comprehension of the nature of the internal structure and motion of glaciers. The first quarter of our century saw an orgy of hypothesizing on conditions prevailing inside glaciers and on the mechanism of glacier flow based on quite insufficient observational and experimental data. Published observations on firn and ice petrography during this period are amazingly few. One can browse through volume after volume of *Zeitschrift für Gletscherkunde* without finding any reference to grain size, air bubbles, etc., of the ice of countless glaciers otherwise described in detail.

Geologists cannot be blamed for this unsatisfactory state of physical glaciology, although they should have been more insistent in demanding the collaboration of specialists from other fields.

Petrologists and mineralogists, however, have not made their just contribution to glaciology, a contribution which would consist in an exhaustive study of the macro- and microstructure of glacier ice and an evaluation of all its struc-

tural features which might throw some light on the mechanism of deformation. There have been no glacial petrologists.

The need for additional data necessary for an adequate theoretical treatment of glacial structure and flow has of course long been realized, but the technical and financial difficulties in obtaining them were not overcome.

Hans Hess made notable attempts to obtain the required data, by means of laboratory work on ice and drilling in glaciers. But he and his colleagues were able to do little more than point in the right direction, toward systematic research on the physical properties of firn and ice, and toward organized group research on the structure and deformation of glaciers by all available means.

The impulse for such research had to come from economic necessity, and it first came in the domain of snow, the raw material for firn and ice.

The advance of technical civilization into alpine valleys in the form of highways, railroads, and winter sports slowly created a demand for control of avalanches. By the early 1930's the demand became imperative, so the Swiss government appointed a Commission of Snow and Avalanches, which obtained the collaboration of the Departments of Geology, Mineralogy, and Hydrology and Soil Mechanics of the Federal Institute of Technology. After years of preliminary research work in the field and in a crude laboratory, under the supervision of Paul Niggli and E. Meyer-Peter (Bader *et al.*, 1938), a superbly equipped research laboratory (Eidgenössisches Institut fur Schnee und Lawienforschung) was built at Weissfluhjoch in 1943, in the snow fields of the Davos skiing region (Bucher *et al.*, 1944; Bucher, 1948). As a result of the work done at Davos by geologists, mineralogists, meteorologists, physicists, and engineers (Anonymous, 1940; 1942; Bader, 1948; Bucher *et al.*, 1940; Bucher and Jost, 1941; Bucher, 1946; Haefeli, 1945; Prohaska and Thams, 1940; De Quervain, 1945; 1948a; 1948b; Thams, 1943), we now have a great deal of knowledge on the structure, metamorphism, and mechanical properties of different types of snow. Haefeli (1938; 1942; 1944; 1947) and Bucher (1947a; 1947b; 1948) have developed the theory of snow mechanics and its application to engineering problems, particularly to avalanche control.

It was inevitable that the men working on snow should become interested in ice and that snow mechanics would lead to ice mechanics and glacier mechanics (Haefeli, 1940; 1948a; Haefeli and Schaerer, 1946).

Here, then, we have one of the sources of renewed interest in physical glaciology.

Another source flows from a very active group of scientists who organized the British Glaciological Society, publisher of the new *Journal of Glaciology* (January 1947). Both the society and the journal owe their existence largely to the unfailing efforts of Seligman, who also pioneered in the study of snow (1936).

In Britain metallurgists are becoming interested in ice (Seligman, 1949), which shows some structural resemblance to metals—it is somewhat analogous to magnesium or aluminum at close to melting-point temperatures. As they cannot study the structure and metamorphism of very hot metals, metallurgists hope to learn something from ice.

In Sweden a group headed by Ahlmann (1948) has for many years been studying the glaciers bordering on the north Atlantic. The accent of this work has been on regime, but currently more attention is being paid to ice structure (Ahlmann and Eroessler, 1949).

I have unfortunately not been able to obtain information on the recent activity of glaciologists in other European counties, and can only refer to two new compilations which should be significant (Drygalski and Machatschek, 1942; Klebelsberg, 1949).

Members of the new European school of glaciology realized the complexity of the task of defining the metamorphism and mechanical behavior of firn and ice masses, and have repeatedly pointed to the low returns of scattered and isolated research by single individuals. If the problem is to be solved, we must work in groups and concentrate our effort on a small number of typical glaciers for a large number of years. A splendid start has been made in the study of the Aletsch Glacier, taking advantage of the facilities of the Jungfraujoch Experiment Station. A number of papers by the British (Perutz, 1940; 1947; Perutz and Seligman, 1939; Seligman, 1941; 1943; 1947) and Swiss

(Haefeli, 1946; 1948b; 1948c; Winterhalter, 1944) groups inform on this phase of the enterprise. Here a recent biological contribution to glaciology deserves mention—pollen analysis. The pollen content of firn varies with the seasons and can be recognized in the ice of the ablation region. Vareschi (1942) has by this method proved that the ogives in the ice streams below Concordia Platz on the Aletsch glacier mark the emergence of annual layers in undisturbed sequence. But the sequence is haphazard (indicating slip thrusting) in the steep, banded layers at the periphery of the glacier and between ice streams originating in the individual firn basins.

Little new laboratory work has been done on ice mechanics, all so far has been on artificial ice at temperatures below the melting point. Perutz (1948) reported on war work at the Cavendish laboratories, and the Weissfluhjoch station is also active. Both laboratories plan more extensive ice work.

Experimentation on wet glacier ice promises to be very difficult as ice-water phase equilibrium is extremely difficult to maintain. Temperatures will have to be controlled to within hundredths of degrees, and very delicate adjustments made when specimens are subjected to hydrostatic pressure and stress. Changes in grain size, grain orientation, air-bubble pressure, and air-bubble distribution will have to be carefully followed. The physical chemistry of the liquid phase at grain boundaries must be investigated. Then there are two liquid phases to be considered—the intergrainal liquid at the grain boundaries, and the intragrainal liquid associated with the air bubbles. The neglected problem of the role of air bubbles and the mechanism of air-bubble elimination will require most careful experimental work. The influence of enclosed rock debris and a host of what now appear to be minor factors will have to be investigated.

The presumably dominant influence of the ice-water ratio on deformational behavior dictates the location of the "warm ice" laboratory in the immediate vicinity of the glacier. Freezing, storing, and transportation of specimens from distant sources would make the value of subsequent testing questionable (Bader, 1949). There is, of course, no such restriction on the installation of facilities for studying natural "cold ice" and artificial ice.

In Switzerland, glaciology has quite recently received a new impulse by attracting the attention of industrial engineers, who command more funds than scientists. In the Alps, water is scarce in winter, when power requirements are at a maximum. So hydraulic engineers have begun to look on firn regions of glaciers as water accumulators, which yield a steady stream during the winter. Fortunately for the glaciologists this water flows off under the whole length of the tongue, and the engineers must place their water intakes in the bed of the glacier in order to minimize loss of altitude. Excavation of tunnels up to 1 kilometer in length is projeceted in several of the larger glaciers of the Valais. Tunnelling in ice has begun (winter 1948–1949), and there is no doubt that we can expect most interesting observations on ice structure and deformation at moderate depth from these developments, as they are being closely watched by glaciologists.

As civilization moves northward in America, glaciers will inevitably create obstacles and hazards, and will also offer benefits. We can predict that glacial and ice engineering will be a profession in the not too distant future, and we must provide its scientific foundation. The organization of glacial research by the Arctic Institute of North America is a most encouraging step in this direction.

Glacial geologists are mapping areas covered by ice sheets and lobes in Pleistocene times. Now glaciologists are requested to provide the third dimension, the thickness of the ice and its flow characteristics. The quality of the answer is important, for instance, in view of the desirability of reliable data on sea-level variations. If a good answer is possible, then it certainly will not be given without computations based on a satisfactory theory of deformation of large ice masses.

I venture the opinion that such a theory is not yet in sight and that many years of extensive, intensive, and expensive laboratory work will be necessary before we can develop one; we cannot hope to do so on the basis of field work alone, but field work must guide the course of laboratory experimentation. We must know the

types of ice to be investigated and the magnitude and type of stresses to be applied.

Large masses of ice are bound to be significantly inhomogeneous due to a number of variables, particularly grain size, which appears to be a function of age (Seligman, 1949). Age may become an important factor in the consideration of large ice sheets and caps.

There are so many things we do not know about ice that a fruitful general discussion is very difficult. Yet the European work outlined above, together with recent American work, provides guidance for future effort. In Alaska, for instance, we have glaciers of a different order of magnitude from those in Europe. We are thus in a position to study the effects of size, for instance whether large size affects not only the magnitude but also the quality of deformation.

The retarded development of physical glaciology fully justifies the renewed activity here summarized. If diligently pursued, it promises results of theoretical significance and practical importance.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

3. BIOGEOGRAPHY OF THE PLEISTOCENE

Part I: Europe and North America

By Edward S. Deevey, Jr.

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INTRODUCTION

Thesis

The problem posed by distributions of animals and plants has been discussed with various degrees of insight since the days of antiquity, but in this field, as in so much of biology, the mid-nineteenth century marks a turning point. Before Darwin and his contemporaries it was easy to suppose that the reason Africa has its hippopotamus, Australia its marsupials and *Eucalyptus*, England its dormouse, and so forth, is simply that species have been created in the geographic regions proper to them. The legend of St. Patrick was not too unsatisfactory as an explanation of the absence of snakes from Ireland. The realization that the origin of species is accessible to scientific inquiry gave new impetus to the study of existing ranges, for it became possible to ask why, since some species are widely distributed, all species are not. Taxonomists of the time of Linné were content to list the habitat of their species in very general terms, particularly when they were exotic—"hab. in partibus orientalis". But at the same time that a less transcendental concept of the nature of species was being crystallized, Humboldt, DeCandolle, Wallace, Dana, and other great biological explorers of the early nineteenth century were paying closer atten-

tion to geographic distribution. As a result it became clear that species spread much or little according, first, to their inherent abilities to disperse, and second, to the intensity of the geographic barriers opposing them.

Greatly increased knowledge of the geologic past, coming at the same time as the revolution in biology, gave prominence in the minds of naturalists to the historic factors in biogeography. Existing species and especially existing stocks are not all of the same age; most invertebrate groups are of Precambrian origin bony fishes arose in the Silurian and Devonian, flowering plants are of Mesozoic age, and the history of modern mammals is a Cenozoic history. The genus is older than the species, the family older than the genus, and all phyla are at least as old as the Paleozoic. It follows that existing ranges of species and of larger groups are the product not of existing geographic conditions but of all geographic conditions obtaining throughout the history of the species or stock.

It might be supposed that the Pleistocene epoch, with its spectacular history of advances and retreats of great continental ice sheets and of contraction and expansion of the ocean, would have received a disproportionate amount of attention from biogeographers attempting to account for existing ranges of species. Not only was the Pleistocene the latest of the geologic epochs, so that its imprint on present-day conditions might be expected to be freshest and most easily legible; it was also, at least in part, very different in its biogeographic implications from the present time—far more different than the Pliocene or the Miocene, for a glacial climatic regime, though not uniquely a Pleistocene phenomenon, is geologically abnormal. It is true that the importance of Pleistocene glaciation in modifying or obliterating the ranges of a large proportion of animal and plant species was clearly grasped by Darwin and Hooker. But later workers have tended to ignore the Pleistocene, or to regard it as of minor and transitory importance, while pursuing the history of stocks of organisms through the more distant geologic past. Engaged in the fascinating pursuit of constructing land bridges across ocean basins or marine channels across continents, they have indulged in flights of irresponsible speculation which have brought the whole science into disrepute. Of the numerous fallacies that underlie the practice of many biogeographers, the most fundamental appears to be that of assuming the existing distribution pattern of the species to be as old as the species itself, or as the genus or family to which it belongs. The fact that species of insects and other arthropods, distinguishable with difficulty or not at all from modern species, occur in the Baltic amber or in the Florissant shales has been widely misinterpreted, and this kind of paleontologic evidence, valuable though it is, has often done more harm than good in distributional studies. The plain fact is that since the species arose, *e.g.*, in the Pliocene or earlier, the Pleistocene has supervened; *there has been sufficient time, and sufficient transfiguration of geography, for the pre-Pleistocene distribution pattern to be completely transformed in a very large number of cases.*

This is the thesis of the present review, and its documentation follows at some length. It is appropriate that this paper, considerably more ambitious than was originally planned, should form part of a symposium on *Interrelations of Pleistocene Research*. Like the distribution of certain animals and plants to be discussed presently, Pleistocene biogeography is *bipolar*. At one pole are grouped ecology, systematic botany and zoology, the study of evolution, and related biologic disciplines. At the other pole are grouped the Earth sciences, all of which are concerned in understanding the geography of the Pleistocene. At present the flow of information from biology to geology is of much lower intensity than in the opposite direction, for biogeographic evidence is often sketchy and speculative. From one point of view, that of Pleistocene stratigraphy, the bipolar pattern breaks down completely, and Pleistocene research becomes one integrated subject, pursued in equal partnership by biologists and geologists in the widest sense. But stratigraphy as such is not under review here; the viewpoint is that of the biologist discussing a geographic problem, for it is recognized that geologists must be shown how biologists can help them. There is no question of the flow of assistance in the opposite direction.

Inadequacy of the Data

The perennial complaint of the biogeographer is that present ranges of species are inadequately known. In part this incomplete knowledge reflects the difficulty of comprehensive collecting, and this problem is more acute with animals than with plants. Yet even for land plants, which usually reveal themselves to the conscientious collector, and do not require to be trapped at night or in their breeding season or when they alight on the ground, novelties, including new species as well as new records, are continually turning up in well-studied regions. But in addition there is the taxonomic difficulty, the perpetual reshuffling and refinement of the taxonomic system that exposes the biogeographer to the constant risk of drawing conclusions from incorrect data. In well-studied groups, such as flowering plants, birds, and mammals, though the demarcation and distribution of species are reasonably well understood, a "microtaxonomy" is coming into existence, in that infraspecific categories (subspecies, races, ecotypes, clones, segregated breeding populations, etc.) are being recognized. The geographic distribution of these smaller taxonomic units presents challenging problems that often, perhaps usually, reflect Pleistocene geographic conditions: witness the work of Dobzhansky and his collaborators with *Drosophila pseudoobscura* populations in the Great Basin, or the cytogenetic studies of Anderson, Turesson, and other botanists. Studies of this sort promise to be more helpful than those carried out on the broader taxonomic lines of species and species groups, but it cannot be denied that they add enormously to the complexity of the data. It seems certain that the systematic catalogue, on which the biogeographer depends for his raw materials, will never be completed.

There are some difficulties about biogeography for which its practitioners themselves, must be held responsible—they are not inherent in the data. One of these, perhaps the most pernicious, may be described as *the synthetic approach*. This is the method by which one sets out to decide the "biogeographic affinities" of a township, a state, an island, a continent, or a body of water. It is a commonplace observation that of the hundreds or thousands of species making up the biota of even the smallest ecologic unit, such as a bunch of prairie grass or a puddle of rainwater in a hollow tree, no two will ever be found to have precisely the same distribution outside that unit. A few may be on or near the exact geometric center of their geographic range, if such a center can be ascertained. Some will be distributed more widely eastward, some westward, some northward, some southward; moreover, there will be disjunctions of some degree in the range of every species. In a steppe region, with patches of vegetation discontinuously distributed on bare ground, it will occasion no surprise that the animals feeding on vegetation do not live on the intervening areas. The faculty of dispersal of the animals is clearly adequate to the situation, and they can fly or jump or run or be carried from one patch to the next. But wider disjunctions begin to arouse wonder, as when the same animal species is found on bunch grass amid sand dunes around the southern shore of Lake Michigan and on the sea coast of New Jersey, with a disjunction, both of animals and of bunch grass, across the intervening region. Confronted with such problems, the human mind embarks on its course of generalization and synthesis, and the biogeographer sits down to describe, in statistical terms, the strength of relationship between regions in respect to the species or genera common to them. He finds that 40 per cent of the species in his area are predominantly of northern distribution, 20 per cent are so uniformly distributed that one cannot tell where they came from, 30 per cent are somewhat more widely distributed to the south, smaller proportions are found to the east or west but not to north or south, and a few show spectacular disjunctions, which may or may not indicate migration from the north whence the plurality of species have evidently come. Since the majority, usually stated as 50 per cent of *analyzable* species, have come from the north, the conclusion is that the connection with the north is beset by fewer geographic barriers, or is of longer duration, or both. Further, the region in question *is a part*, biogeographically if not otherwise, of the larger region to the north, and may be combined with it as a super-region or province or realm.

This procedure was essentially that of Wallace, and with the occurrence of certain charac-

teristic types in certain areas and their absence in all others (*endemics:* marsupials in Australia, etc.) led to the recognition of the classic biogeographic realms, Palaearctic, Oriental, Australian, Ethiopian, Nearctic, and Neotropical. As terms these are very useful, since they express certain facts of biogeography that would be very cumbersome if expressed in terms of political geography. As concepts, unfortunately, they leave little more to be said; they have served poorly as a basis for further research. The great majority of modern biogeographers seem to be engaged in further refinement of Wallace's realms, breaking them down into provinces and subprovinces, the boundaries of which inevitably differ according to the kind of organism considered. Except perhaps in discussing the land biota of islands, it is an essentially fruitless pursuit, since it is based on the generalization of facts that cannot be generalized.

To see that this is so, we need only consider the small balance, 40 against 30 per cent, or 50 against 38 per cent of analyzable species, by which northern affinities are said to be demonstrated in the above hypothetical example. Some of the excess may be due to species that move together, like cows and cowbirds, insects and their food plants, parasites and hosts; the southern contingent may happen to be poorer in such associations. Again, the synthesis may overlook the fact that the southern component is more largely made up of species that can migrate with great difficulty—slugs, flightless beetles, and plants with no special means of seed dispersal. If we suppose the area was submerged under the sea, and then uplifted and exposed to simultaneous immigration from northern and southern areas of equal size and equal number of species, it might well turn out that the species that arrived from the south are many times more remarkable, being flightless, than the species that flew in from the north. But a more fundamental objection than these is that the synthesis ignores the matter of time. The true situation may be that the whole of the biota of this region came from the south, but that there was an earlier wave of migration that produced the 40 per cent of species whose southern ranges have since been obliterated. After an interval that may or may not be indicated by the age (degree of specific differentiation, etc.) of the species, a second wave of migration came from the south and is still coming. In short, the synthetic approach obscures some of the most interesting questions of biogeography, and "faunal elements" are quite likely to be meaningless abstractions.

Another defect of biogeography as practiced at least until recently is the failure of most biogeographers to appreciate the potential abilities of species to spread. Because of this failure, as Mayr, Darlington, Dammerman, and others have recently pointed out, it is now necessary to rewrite most classic biogeography. The vast majority of former land bridges constructed in imagination are not only in direct conflict with the far more reliable data of physical geology, but they can easily be shown to be unnecessary. A few kinds of animals, and perhaps a few plants, really seem to require continuous land connection for their dispersal, and it is impossible to imagine their crossing a water gap of appreciable dimensions. The occurrence of elephants and rhinoceroses in the Pleistocene or recent fauna of Java, Sumatra, the British Isles, and other truly continental islands clearly implies a dry-land connection in the past. Intercontinental land connections across Bering Strait and along the Isthmus of Panama are fully demonstrated by zoogeographic evidence, and the same evidence shows that South America was separated from North America for a long interval during the middle Cenozoic, and connected again in the Pliocene. Genuine bridges of this kind, abundantly supported by geologic evidence, are of course not in question; they have been amply discussed by Matthew (1915) and more recently by Simpson (1940; 1943a; 1943b; 1947). But the more tenuous bridges of biogeography, such as the one that is supposed to have connected Fiji with the Asiatic mainland (to account for the presence of frogs in Fiji), or the one said to have spanned the Pacific Ocean (to account for the occurrence of leptodactylid frogs, marsupials, etc., in Australia and South America), or the celebrated *Hipparion* bridge across the North Atlantic Ocean, are being dispensed with. The temptation to construct them is always with us: a remarkable bridge is supposed to have connected the deserts of California and Peru, to

account for the common occurrence of certain genera of beetles unknown in intervening (non-desert) regions (Van Dyke, 1940). For reasons not altogether clear, the bridge that now connects these two deserts is unsatisfactory, so a new one, paralleling the present one but somehow avoiding the humid tropics, has to be erected. But modern biogeography has been enriched by several works emphasizing the ease, rather than the difficulty, with which land organisms can cross water barriers. Notable among these is the painstaking study of the recolonization of Krakatau in the 50 years since its fauna and flora were destroyed by a colossal volcanic explosion (Dammerman, 1948). Mammals other than rats and bats are still lacking on Krakatau, which lies in the Sunda Strait between Java and Sumatra, but comparative studies show that the fauna is already nearly as harmonious as could be expected on an island of its size and geographic situation. The outstanding conclusion is that recolonization in such a case is not so much a matter of accident (as it certainly is on the more remote oceanic islands) as of ecologic succession, and that as soon as living conditions (vegetation, soil, etc.) are suitable for the survival of an animal species, that species appears. Transportation of animals by air currents has also been discussed recently by Gislen (1948), whose review, accompanied by numerous references, ought thoroughly to confound the more irresponsible builders of land bridges.

Inadequacy of the Coverage

Apart from numerous deficiencies of the biogeographic information as it exists and as it is handled by biogeographers, this review of Pleistocene biogeography suffers from inadequate preparation on the part of its author. The enormous extent of the literature of this subject is not commonly realized even by biologists. Annual bibliographies for the years 1931 through 1934, prepared by Rensch and appearing in the journal *Zoogeographica*, average 200 titles apiece, though they are surely incomplete. Strictly phytogeographic papers are at least equally numerous. The great bulk of this material is embedded in taxonomic works, for nowadays virtually every taxonomist feels called upon to discuss biogeographic questions in most of his major articles. A complete bibliography of the subject since 1900 would doubtless run to over 100,000 titles, and would of course be completely unusable. Faced with this terrifying mass of information and misinformation, the author, who is not an encyclopedist, has decided to make no pretense at complete coverage. A small number of standard works on the Pleistocene (Woldstedt, 1929; Flint, 1947; Zeuner, 1945; 1946; Movius, 1942) and on biogeography (Cain, 1944a; Mayr, 1942) have been freely consulted, and excursions into the periodical literature have been rather desultory, carried out with the idea of documenting some of the leading problems of biogeography insofar as they bear on Pleistocene events. Valuable reviews of certain subjects not touched upon in the standard books may be found in the three published volumes of *Zoogeographica* and the eight *Mémoires de la Société de Biogéographie*, particularly No. 2 (high mountains of the Old World), No. 3 (British Isles), and No. 6 (Old World deserts). Phytogeography, as distinct from zoogeography, has not been deliberately slighted, but the author is a zoologist who happens to know something about postglacial pollen analysis, and apart from this rather specialized field the botanical side of this review will inevitably strike a botanist as spotty and unsatisfactory.

A Few Principles

In order that biologists may understand the author's fundamental position on matters of biogeography, a few of the guiding principles of the subject are presented as they appear to him. Ignorance of these principles vitiates much biogeographic discussion, and their statement may provide an excuse for apparent neglect of certain supposedly important works.

(1) *We deal with species*, not with families or orders. The basic datum of biogeography is conceived to be a map showing the range of a species. Usually the ranges of the closest relatives of a species also need to be known. Syntheses of distributions of larger taxonomic categories ordinarily conceal more than they reveal; in any event, deductions from such distributions relate to a past geography far antedating the Pleistocene, and have no place in this review.

(2) *The age of a distribution pattern is not necessarily the same as the age of a species.*

(3) *Economy of hypothesis.* No distribution is taken to be old unless it can be proved not to be young. The recolonization of glaciated areas is assumed to be postglacial, as the simplest hypothesis, unless it can be proved otherwise. All distributions of species are taken to be of Pleistocene date in the absence of good proof that they are older.

(4) *Center of origin.* There is no infallible criterion by which to decide where a species originated. The center of origin of a genus is usually taken to be the region in which the largest number of species occurs. This is an unproved assumption and may be erroneous. In fact, as Darlington (1948) has pointed out, if contracting stocks are about as common as expanding stocks, biogeographers who rely on this criterion will be wrong about half the time. The relation between parent and offspring species can sometimes be decided on purely morphologic grounds, though not so often as some systematists think. Often, and especially in plants, relationships of polyploidy and other genetic information make it possible to be certain on this score. But the present range of the parent species is not necessarily the place of origin of the offspring species. (For full discussion of criteria of center of origin, *see* Cain, 1944a.)

(5) *Origin of species.* Modern genetic and ecologic theory are in full agreement that species do not arise from other species except through reproductive isolation of segments of a parental population, and that in sexually reproducing animals and plants the reproductive isolation is ordinarily achieved through geographic segregation. For modern views on the mechanism of the origin of species, the works of Dobzhansky (1941), Mayr (1942), Huxley (1943), and (most painlessly) Lack (1947) may be consulted. The point to remember for biogeographic purposes is that the occurrence of closely related species in the same general region implies their differentiation in previous isolation; this isolation must have lasted long enough, first, to produce the reproductive divergence necessary to avoid swamping of one by the other, and, second, to produce the ecologic differentiation (differences in food habits, temperature preferenda, etc.) necessary to avoid too stringent competition. Nearly all well-studied cases of subspeciation and speciation point to the Pleistocene as the time of such previous isolation, and the occurrence of closely related forms in the same area is therefore attributed to post-Pleistocene alterations in geography and in biogeography.

Pleistocene Biogeography of Europe

Introductory Remarks

Though the idea that the Ice Age was somehow concerned in the origin of the boreo-alpine distribution of organisms goes back at least as far as Edward Forbes, the general problem of Pleistocene influence on a pre-existing fauna and flora can best be stated in the words of Darwin (*The origin of species*, 1936 ed., p. 290):

> "As the cold came on, and as each more southern zone became fitted for the inhabitants of the north, these would take the places of the former inhabitants of the temperate regions. The latter, at the same time, would travel further and further southward, unless they were stopped by barriers, in which case they would perish. The mountains would become covered with snow and ice, and their former Alpine inhabitants would descend to the plains. By the time that the cold had reached its maximum, we should have an arctic fauna and flora, covering the central parts of Europe, as far south as the Alps and Pyrenees, and even stretching into Spain. . . .
>
> "As the warmth returned, the arctic forms would retreat northward, closely followed up in their retreat by the productions of the more temperate regions. And as the snow melted from the bases of the mountains, the arctic forms would seize on the cleared and thawed ground, always ascending, as the warmth increased and the snow still further disappeared, higher and higher, whilst their brethren were pursuing their northern journey. Hence, when the warmth had fully returned, the same species, which had lately lived together on the European and North American lowlands, would again be found in the arctic regions of the Old and New Worlds, and on many isolated mountain-summits far distant from each other."

Since Darwin's day it has been possible to document this general idea in great detail. What has chiefly been added is a fuller knowledge of multiple glaciation during the Pleistocene. There was not one Ice Age, but several. In the interglacial ages many species wandered far north into Europe and have since retreated to the Balkans (like *Rhododendron ponticum*) or into Africa (lion, hippopotamus, rhinoceros, *Corbicula consobrina*). Many that have become

extinct in Europe, either early (mastodons, hemlock) or quite late in the Pleistocene (*Brasenia purpurea*, *Dulichium spathaceum*, musk ox), still survive or became extinct much later in North America, presumably because in North America there was no transverse system of mountain ranges blocking their southward dispersal during glacial ages. Thus eastern North America has preserved a larger proportion of the old "Tertiary relict" genera (magnolia, sweet gum, hickory, walnut, salamanders, bowfin, gar-pike) than has Europe, and during the Pleistocene received in addition a contingent of the remarkable South American mammalian fauna (ground sloths, glyptodonts), some of which still survive (opossum, armadillo). During glacial ages, on the other hand, the reindeer and the musk ox ranged widely over northern Europe at least as far south as southern France, the great auk and the alpine chough were found at Gibraltar, and the boreal mollusk *Cyprina islandica* lived in the Mediterranean.

Omitting the details of the stratigraphy, which are not the subject of this paper, the modern work on European biogeography is devoted to two major problems, which will be discussed in turn: the recolonization of central Europe, including the origin of the boreo-alpine distribution pattern, and the recolonization of the British Isles. The main outlines of the stratigraphy are given in Tables 1 and 2, and the lateglacial and postglacial stratigraphy is considered in some detail in the following section. Only against a background of this sort of information does an account of existing ranges of species yield any data that could not have been deduced by Darwin and his contemporaries.

The Last Glaciation and After

Earlier glaciations.—The main outline of the Pleistocene stratigraphy of Europe is given in Table 1, which emphasizes northern Europe, the best-known region. The view that three major glacial ages are recorded—Elster, Saale, and Warthe-Weichsel—and that they correspond to Mindel, Riss, and Würm of the Alpine sequence is rather generally accepted. The controversial character of the Early Glaciation (Günz) does not concern us here; it is difficult to distinguish glacial from interglacial in deposits of this age along the British North Sea coast, though the main part of the Cromer sequence is certainly interglacial. Zeuner's attempt to show that the "Early," the "Antepenultimate," and the "Penultimate" glacial ages were bipartite, interrupted by short interglacial subages, though helpful in many respects, is still too little agreed upon to serve as the basis for a general synthesis. Many workers feel that it represents an unconscious effort to make the geologic facts fit a scheme deduced from the radiation hypothesis of Milankovitch, against which strong objections have been urged on astronomic as well as meteorologic grounds.

Pollen data are probably the most instructive for interpreting the climatic character of interglacial ages. They have one disadvantage—the pollen may be blown into a deposit from a considerable distance, especially if the locality is unforested, so that the species recorded may actually have been living no nearer than 500 miles to the site. But balanced against this is the elegant stratigraphic refinement made possible when layers a centimeter or so apart yield consistent and meaningful differences in flora. Pollen analysis is now available for many of the interglacial deposits of Europe, some of them exceedingly important and well worked out, but far too few of them can as yet be assigned an incontrovertible stratigraphic position. An excellent guide here is Gams, whose paper (1935) seems to be inadequately known; it reproduces in convenient form the pollen diagrams from most of the important sites. Gams calls the three major interglacials "C" (Cromerian), "D" (Dürntenian), and "E" (Eemian). The "Aurignacian oscillation" is regarded as intra-Würm (Warthe-Brandenburg). The propriety of the names is open to question: the Dürnten deposit is in the Alps, and may not belong to the second interglacial age, and it seems inadvisable to use an archaeologic name (Aurignacian) for a geologic horizon, no matter how conclusive the evidence for association. But no animal or plant is so sure a guide fossil to this interval as Aurignacian man, and no name (alternatives: Warthe-Brandenburg, Würm I- Würm II, "F" (Rixdorf)) is of such general meaning in northern Europe.

The "C" interglacial, which is the age of the Cromer Forest Bed, Tegelen, Mosbach, and Mauer, seems to be represented pollen-analyti-

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TABLE 1.—CONDENSED STRATIGRAPHY FOR GLACIATE

Chiefly after Gams (1935) and

Glacial and Interglacial Stages	Flora	Fauna	
Bothnian Scanian Pomeranian		See Table 2 for chro	
Brandenburg			
'Aurignacian" Oscillation		Rixdorf Horizon: rich mammalian fauna. Skärumhede: boreal marine mollusks. Cold steppe fauna, but not throughout	B
Warthe			(E Se
"E" Interglacial	Age of mixed oak forest, essentially as today: hornbeam, hazel, alder. "Tertiary relicts" in W. Europe: *Thuja occidentalis* *Fraxinus* cf. *americanus* *Juglans* sp. *Ilex occidentalis* Last appearance of *Brasenia purpurea*	Eem warm marine fauna. Age of *Ursus spelaeus*, *Felis leo spelaea*. Last appearance of *Elephas antiquus*. Lower travertine of Ehringsdorf: bear, wolf, fox, badger, lion, beaver, rhino, ox, fallow deer, etc., etc.	
Saale		Rise of *Elephas primigenius* Immigration of *Tichorhinus antiquitatis*	
"D" Interglacial	Age of oak-ash forests, with alder in maritime regions, some beech farther westward *Tsuga* cf. *canadensis* still present *Rhododendron ponticum* in Alps Other "Tertiary relicts"	Age of *Elephas antiquus* *Paludina* horizon at Berlin Last appearance of hippo	N D
Elster		Reindeer, musk ox, *Elephas trogontotherii* on steppes; Last appearance of *E. meridionalis* and other Pliocene survivors	
"C" Interglacial	Tegelen: elm, ash, maple, hornbeam, grape, magnolia *Picea omorikoides* on Lüneburg Heath	Tegelen: *Paludina diluviana*, *E. antiquus*, *E. trogontotherii*, hippo, hyaena, *Equus stenoni* Mauer: *Dicerorhinus etruscus*, *Machairodus*, *Cervus elaphus*, etc. Age of "archaic" mammals Extension of *Corbicula fluminalis*, *Belgrandia* (=*Paludestrina*) *marginata* to North Sea coast	H
First Glacial		Mastodon, *Elephas planifrons* die out in Europe	

IGRAPHY FOR GLACIATED REGIONS OF CONTINENTAL EUROPE
after Gams (1935) and Zeuner (1945)

una	Pollen Sequences		
See Table 2 for chronology of Last Glaciation			
h mammalian fauna. l marine mollusks. but not throughout	Brörup, Jutland	Birch rising Hazel, alder, mixed oak Birch falling	A cold b maximu especial
	(Herning Series)	Danish (Subarctic) Middle Bed	
fauna. *us, Felis leo spelaea.* *Elephas antiquus.* f Ehringsdorf: bear, lion, beaver, rhino, c., etc.		Birch rising Alder, hornbeam Mixed oak (Eem transgression) Subarctic Tundra	A short, n about t
nigenius *horhinus antiquitatis*			Apparentl as Last
quus t Berlin hippo	Neu-Ohe, Lüneburg Heath; Dzbanki, Poland	Subarctic taiga 2nd mixed oak (in west) Long alder phase (in west) Mixed oak (very high in Germany) Alder, hazel, pine Subarctic birch tundra	A long, v haps wi warmer
, *Elephas trogonto-* *E. meridionalis* and rvivors			Widespre ranges, cies, mo
diluviana, E. anti- *erii*, hippo, hyaena, *us etruscus, Machai-* *hus*, etc. ammals *cula fluminalis, Bel-* *lestrina) marginata* t	Hamarnia, Poland	Return of conifers (spruce, pine) Mixed oak maximum *Pinus silvestris*, rise of mixed oak Subalpine pine declines Pine, birch, willow	A definite though than to
planifrons die out			

	Remarks
	A cold but not glacial interval; maximum as warm as today, especially in Britain
ed	
)	A short, mild interglacial, climate about the same as today
	Apparently not so long or severe as Last Glaciation
er-	A long, warm interglacial, perhaps with cool oscillations, but warmer at times than today
	Widespread readjustment of ranges, extinction of a few species, mostly Pliocene survivors
ne) ak	A definite interglacial, as warm though probably not warmer than today at climax

ically by a deposit at Hamarnia, Poland (Szafer and Trela, 1929; Szafer, 1931). The primary references for the rest of the pollen column in Table 1 are: Neu-Ohe on the Lüneburg Heath, Gistl (1928); Dzbanki, Poland, Premik (1932) and Piech (1932); Herning Series, Jessen and Milthers (1928). The paper of Jonas (1937a) on the very important deposit at Quakenbrück in northwestern Germany may be consulted for further information on the "D" interglacial. A peat deposit, 1 meter thick and showing a pollen sequence comparable to the major part of the Neu-Ohe diagram, has recently been described by Pfaffenberg (1939) and Dewers (1939) at Haren in the Ems valley. Jonas (1937b), who has also investigated the pollen here, assigns this deposit to the "C" interglacial and correlates it with the upper part of the Hamarnia diagram.

The outstanding fact about these pollen sequences is of course their similarity to postglacial diagrams. Many of them begin with an arctic or subarctic horizon, attested by pollen or macroscopic specimens of dwarf birch, arctic willow, etc.; a phase of pine forest with hazel coppices follows, and the warmth maximum of the interglacial age culminates in a phase of mixed-oak forest (oak dominance with varying percentages of lime and elm pollen) with significant amounts of alder in more maritime situations; then follows a return of conifers and a gradual re-establishment of subarctic or arctic conditions. In one of the interglacials, taken by Szafer (1925) to be the last, but probably to be regarded as the second (Piech, 1932; Gams, 1935), the succession of floras was quite as complicated as that of the postglacial, and Szafer (1929) used the Blytt-Sernander names for the pollen phases. In other words the climate of the "C", "D", and "E" interglacials progressed from cold to as warm as today and back to cold again, while the middle one seems to have been the warmest as well as the longest.

The Warthe-Brandenburg Interval.—Adopting the reasonable though not universal view that the Warthe glaciation was part of the last glacial age (Movius, 1942; Flint, 1947), thus corresponding to the Iowan in North America, we have the correlation presented in Table 2. In post-Warthe time the ice must have retreated a considerable distance before readvancing. The interval between the glaciations represented by the Fläming and Brandenburg moraines was probably not quite so warm as today, nor so warm as the "E" interglacial with its warm-water mollusks in the Eem Sea. But during at least part of the interval a temperate climate prevailed in northern Europe south of the Baltic. As evidence of this there are fossil floras: at Kirmington, Yorkshire (Burchell, 1935); Burn of Benholm (Campbell and Robertson, 1934) and Cowdon Burn (Bennie, 1891) in Scotland; Brörup in Jutland (Jessen and Milthers, 1928); Marga Ditch near Senftenburg in central Germany (Firbas and Grahmann, 1928); Grodno in Poland (Jaron, 1933); diagrams for the last three are in Gams (1935), while the first three are discussed by Movius (1942). There are also the temperate or boreal but not arctic marine mollusks in the estuarine silt at Kirmington (Wright, 1937; Movius, 1942) and in the marine deposits of the March-Nar Sea in the British Fenlands (Baden-Powell, 1934) and at Skärumhede in Jutland (Jessen and Milthers). This is the age of the Rixdorf horizon, which contains mammals indicative of arctic conditions (mammoth, musk ox) as well as such southern species as the lion and the hyaena; this rich mammalian fauna is surely not all of the same age within the interval. In the regions peripheral to the Alps and especially at the Aurignacian stations themselves, most of which are caves, the mammalian fauna as a whole points to a cold climate; again, not all faunas associated with Aurignacian man are of the same age as the mixed-deciduous floras recognized at the climax of the interval.

The Daniglacial Interval.—Few fossiliferous horizons can be assigned to this phase with any confidence, and its climatic character is correspondingly little known. In England, this is supposed to be the age of the St. Bees and Holmpton peats, the First Retreat (after the New Drift glaciation) as recognized by Movius. The peat at St. Bees, overlain by till taken to be that of the Scottish Readvance, contains a miscellaneous collection of plant remains, determined by Miss M. E. J. Chandler: *Eleocharis uniglumis*, *Menyanthes trifoliata*, *Hippuris vulgaris*, *Empetrum nigrum*, *Lychnis flosculi*, *Stellaria palustris*, *Potentilla tormentella*, *P. comarum*, *Primula farinosa*, *Alisma plantago*, several sedges, etc. A similar assem-

blage of species could be picked in the Lake District today, according to Miss Chandler (Eastwood and others, 1931, p. 244–245). At Holmpton in Holderness (Reid, 1885) fresh-water mollusks of a nondescript character underlie a bed containing dwarf birch. On the other hand, if this was the age of the "Masurian interstadial" (Hess von Wichdorff, 1916; Menzel, 1916), some deposits of this age point to somewhat cooler conditions; at least *Planorbis borealis*, a fresh-water mollusk of northern distribution, was found in an otherwise nonindicative fauna (*Limnaea stagnalis, peregra, truncatula, ovata, mucronata*, species of *Valvata, Sphaerium, Pisidium, Anodonta*, and scales of perch (*?Perca flavescens*)). The flora, according to Stoller (cited in Woldstedt, 1929) includes dwarf birch, dwarf willow, and alder. The flora seems to be colder than the fauna, but when one considers that the dwarf birch occurs today in Baltic Germany, though admittedly as a relict (Overbeck and Schneider, 1938), it cannot be thought of as proved that the Masurian interval was colder than Poland today, though no one would say it was warmer. Gross (1937), however, maintains that the "Masurian interstadial" is not a stratigraphic unit, but a complex of deposits of various ages within the late-glacial of East Prussia, including some Allerød layers.

Evidence of the reality of the First Retreat of Movius is rather slender, and the deposits discussed here may belong to other episodes. There have been several reports, however, of double oscillations of Allerød character (Gross, 1937; Godwin, 1947), and the older one may prove to be of Daniglacial age as here defined.

The Gotiglacial Interval.—With the waning of the ice sheets after the glacial episode represented by the Pomeranian moraines and the Scottish Readvance we are on familiar ground, and from this time onward the stratigraphic picture is rather detailed. One cannot feel so sure about the Gotiglacial or Second Retreat as of later episodes, but it is generally accepted that that the Allerød oscillation belongs to this interval and that it represents a phase of postglacial warmth and reforestation of northern Europe the Allerød oscillation belongs to this interadvance of the ice. The most conspicuous evidence of the readvance comes from the Salpausselkä end moraines in Finland. In a broad belt of country distal to the Fennoscandian moraines and stretching from Ireland to Finland and probably to Russia, sections of peat bogs and lake deposits frequently contain, just above the bottom, significant quantities of pine and birch pollen, often with macroscopic remains of these and other species. The flora points to a cool-temperate climate that permitted light forest development in places. At the type site of Allerød (Hartz and Milthers, 1901) and elsewhere deposits of this sort are intercalated between two layers (Older and Younger Dryas) carrying *Dryas octopetala* and other arctic plants. General references to the Allerød problem are by Gross (1937) and Gams (1938). The British Isles have been brought into the group of countries having Allerød deposits rather recently, with the report of Jessen and Farrington (1938) on the Ballybetagh site in Ireland, and the working out of the lake development of Windermere by Pennington (1947). Allerød deposits are now known also from France (Dubois and Dubois, 1944), and from western Norway (Faegri, 1936).

In the Baltic basin the Baltic Ice Lake came into existence during the Gotiglacial interval; its fauna is poorly known, according to Ekman (1933b), though it includes a cold-water catfish, *Siluris glacialis*, from deposits near Leningrad. Outside the Baltic, if we follow Movius' account, the Late-Glacial Sea was "the British and Irish counterpart of the Yoldia Sea of the Baltic" (1942, p. 60). On the evidence given by Movius, however, this cannot be strictly true: the Yoldia Sea was later and colder than the sea of the Gotiglacial interval. Detailed evidence from marine deposits on the southern Scandinavian North Sea coast, summarized by Ekman (1933b), shows that an arctic fauna, including *Pecten islandicus, Portlandia intermedia*, and *Macoma calcarea* (relatively warm-water mollusks) in addition to the high-arctic *Portlandia* (=*Yoldia*) *arctica*[1] and *Arca glacialis* was succeeded by a fauna containing *Mytilus edulis, Littorina littorea, Zirphaea crispata*, and the barnacle *Verruca stroemia*. This fauna was in turn

[1] This is the type fossil of the "Yoldia" Sea; unfortunately it is not a *Yoldia* at all. The distribution and ecology of this nuculid mollusc have been competently summarized by Jensen (1942). The typical *Leda* species of the "Leda Clays" of New England and the Maritime Provinces, which are doubtless of approximately the same age and significance as the Yoldia deposits, are closely related

TABLE 2.—CHRONOLOGY OF NORTHERN EURO

Chiefly after Movius (1942), with additions: Aario (1943); Dokturowsky (1938); Firbas and Grahmann (1928); Godwin (1940; 1943); (
and Schneider (1938).

GLACIAL CHRONOLOGY Northern Europe	GLACIAL CHRONOLOGY British Isles	STAGES OF THE BALTIC	GREAT BRITAIN				
			Irish Zones		English Zones		Danish Zones
			VII	Alder-oak-elm-birch-beech	SUB-ATLANTIC		
					VIII	IX	
			VI		SUB-BOREAL		
					VII–VIII	VIII	
		Littorina Sea	Vb	Alder-oak-elm-lime (Climatic Optimum)	ATLANTIC		
					VII	VII	
Ragunda		Ancylus Lake	Vb	Pine-hazel Mixed-oak begins	VI	VI	
					BOREAL		
FINIGLACIAL	THIRD RETREAT		Va	Pine, with birch Hazel begins	V	V	
			IV	Birch-pine, with willow and much herbaceous pollen	PRE-BOREAL		
		Yoldia Sea			IV	IV	
			III	Arctic-alpine plants at Windermere	III	III	
Fennoscandian	Valley glaciation of Scotland, Ireland; Wicklow	Baltic Ice Lake / Late-Glacial sea outside Baltic	II	Windermere; Birch-pine-aspen woodland; lake mud, peat, with subarctic or cool-temperate plants, beetles	ALLERØD		
					II	II	
GOTIGLACIAL	SECOND RETREAT						
Pomeranian (Würm III)	Scottish Readvance	Still covered by ice	I		I	I	
DANIGLACIAL	FIRST RETREAT	Ice receding	St. Bees Peat: flora like Lake District today ? Chara mud at Ballaugh				
Brandenburg (Würm II)	New Drift glaciation (Hunstanton-Hessle)	Covered by ice	Extinction of mammoth and wooly rhino				
AURIGNACIAN INTERVAL (Würm I/Würm II)	AURIGNACIAN INTERVAL	Fennoscandia may have been an island	Later marine (March-Nar) transgression: Estuarine silt at Kirmington: Boreal molluscs—*Tellina balthica*, cockle, mussel, *Scrobicularia*, etc. March deposits: *Tellina balthica*, *T. calcarea*, *Cyprina islandica*, *Corbicula fluminalis*, oyster, limpet, periwinkle				Skaerumhe Boreal mar molluscs
			Pollen at Burn of Benholm; pine-birch to birch-pine, alder and oak throughout				
			Early emergence: peat at Kirmington: Alder, birch, pine, spruce, oak, lime, elm, holly, ash, hazel Fresh-water clay at Kilmaurs: Mammoth, reindeer, pondweeds, crowfoot, etc.				
Warthe (Würm I)	Old Drift glaciation (Upper chalky boulder clay)	Covered by ice					

TABLE 2.—CHRONOLOGY OF NORTHERN EUROPE FROM THE LAST GLACIATION TO THE PRESENT

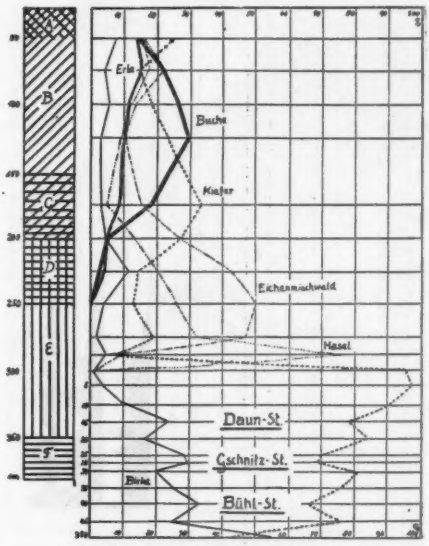
); Firbas and Grahmann (1928); Godwin (1940; 1943); Godwin and Clifford (1938); Hess von Wichdorff (1916); Jessen (1935); Jessen and Milthers (1928); Menzel (1916); Nilsson (1935); Overbeck

GREAT BRITAIN			DENMARK	SCANIA		NORTH GERMANY		FINLAND	RUSSIA
	English Zones		Danish Zones	Scanian Zones		N. German Zones			
Alder-oak-elm-birch-beech	SUB-ATLANTIC	VIII IX		I	Beech forests spreading	XI	Beech-hornbeam	Pine-spruce-birch	Spruce-birch-pine
			Grenz-Horizont						
	SUB-BOREAL	VII–VIII VIII	Declining Mixed-oak; Second pine peak; Hornbeam, beech	II	Beech forests spreading	X	Oak-beech	Spruce-pine-birch	Pine
				III	Transition		Hazel declining	Mixed-oak declining	Spruce spreading Mixed-oak declining
Alder-oak-elm-lime (Climatic Optimum)	ATLANTIC	VII VII	Oak-elm-lime (Climatic Optimum)	IV	Late mixed-oak forest Elm declining	IX	Oak phase of mixed-oak-hazel zone	Pine-birch-spruce	Mixed-oak maximum; Alder, hazel, beech Spruce spread begins
				V	Early part of fully developed mixed-oak	VIII	Lime-elm phase of mixed-oak-hazel zone	Mixed-oak maximum	Birch dominates early
				VI	Transition				
Pine-hazel Mixed-oak begins	BOREAL	VI VI	Pine-hazel Mixed-oak begins	VII	Spreading of alder, mixed-oak	VII	Hazel-pine Alder begins	Pine-birch;	Birch-pine in west, with alder, spruce, some mixed-oak
Pine, with birch Hazel begins		V V	Inflection of alder curve Pine	VIII	Hazel woods, with pine	VI	Pine-hazel Mixed-oak low	Alder, elm, hazel	Pine-birch in central part
Birch-pine, with willow and much herbaceous pollen	PRE-BOREAL	IV IV	Pine, with herbaceous pollen	IX	Birch-pine	V	Birch Beginning of warm phase	Birch-pine	Pine, birch, alder, willow
Arctic-alpine plants at Windermere	III	III	Upper *Dryas* flora Birch-pine pollen	X	Upper *Dryas* flora	IV	Birch-pine or pine-birch	? Upper *Dryas* flora	
Windermere; Birch-pine-aspen woodland; lake mud, peat, with subarctic or cool-temperate plants, beetles	ALLERØD	II II	Pine-birch pollen, with some temperate hardwoods Mud, peat, with *Betula pubescens*, *Pinus silvestris*, and willow	XI	Allerød Oscillation Open birch woods with pine	III	Allerød Oscillation, open birch-pine woods	Herbaceous pollen declines, spruce appears Birch-pine ? Lower *Dryas* flora	First spruce maximum Birch-willow (tundra)
	I	I	Lower *Dryas* flora Birch-pine pollen	XII	Birch-pine Lower *Dryas* flora	II	Subarctic birch		
						I	Treeless tundra		
Peat: flora like Lake District mud at Ballaugh						Masurian Interstadial ? Dwarf birch, dwarf willow, alder			
on of mammoth and wooly rhino									
arine (March-Nar) transgres-									
e silt at Kirmington: l molluscs— *a balthica*, cockle, mussel, *Scrobi- a*, etc. eposits: *a balthica*, *T. calcarea*, *Cyprina ica*, *Corbicula fluminalis*, oyster, , periwinkle		Skaerumhede: Boreal marine molluscs	Pollen at Brörup—(Herning Series) Birch rising			Pollen at Marga, Saxony	5. Pine forest 4. Birch stage 3. Pine forest with oak, lime, elm, beech, fir, alder, hazel		
t Burn of Benholm; pine-birch h-pine, alder and oak through-			Hazel, alder, mixed-oak						
nergence: peat at Kirmington: birch, pine, spruce, oak, lime, olly, ash, hazel ater clay at Kilmaurs: Mam- reindeer, pondweeds, crowfoot,			2. Birch steppe 1. Pine forest Birch falling						

succeeded by a true *Portlandia* (high-arctic) fauna of Finiglacial age, and this is the horizon that corresponds to the Yoldia Sea of the Baltic. The list of mollusks given by Movius as typical of the British Late-Glacial Sea contains *Pecten islandicus*, *Cyprina islandica*, *Astarte borealis*, *A. compressa*, *Yoldia norvegica*, and *Macoma calcarea*. None of these can be called high-arctic, while *Cyprina islandica* is not even arctic, but boreal. Thus the marine fauna of the Gotiglacial North Sea plainly points to an amelioration of climate of Allerød type, and the British Late-Glacial marine horizons should be re-examined for a more detailed stratigraphy.

The Late-Glacial.—In regions relatively far from the outer limits reached by the last ice sheet, as for example southern Germany, it is not to be expected that late-glacial stratigraphy should correlate in every detail with that of more northern districts. The climatic deterioration represented by the Upper Dryas flora in Denmark that followed on the Allerød oscillation was local, in the sense that the influence of the readvancing ice did not penetrate very far beyond the ice itself, and the vegetation of periglacial regions was already in a "postglacial" stage of development, though an early one. In Swabia and Bavaria the proximity of the Alps introduces a complicating factor, for the retreat of the Würm ice sheet was marked by halts and temporary readvances, and these were probably synchronous with similar events in the Baltic region only in a general way. Reciprocal oscillations of the curves for pine and birch pollen have usually been understood as indicating interruptions in the deglaciation, as shown in a boring from the Pfrunger Ried on the Württemberg-Bavaria boundary (Fig. 1), the birch representing a cold phase, the pine a warmer interval. Such oscillations, though useful locally, are not likely to have taken the same course everywhere in the Alps, and correlation with similar events in districts affected by the Scandinavian ice sheet is difficult if not impossible. It is clear that the pine-birch phases found at the bottom of nearly every central European pollen profile, though postglacial in the strict sense of the word, are really of late-glacial age, for there was ice both to north and to south.

Accordingly, a Late-Glacial phase is distinguished, in central Europe, from the Postglacial. In some respects this is unfortunate, for in any chronology based on glacial retreat the length of postglacial time must vary according to the locality, and in a logical terminology



A = Moorerde, B = Torf, C = Torfmudde, D = Lebermudde, E = Seekreide, F = Ton.

FIGURE 1.—POLLEN DIAGRAM FOR A BORING IN THE PFRUNGER RIED, A SWAMP ON THE WÜRTTEMBERG-BAVARIA BOUNDARY
From Fr. Bertsch, 1935, Abb. 8.

"postglacial" would be used only in a local and relative sense. But as stratigraphic refinement of "postglacial" time is attained, it becomes necessary to distinguish a time when the flora and fauna were influenced by the presence of near-by ice from a time when they were not. For the present, and until an absolute chronology is available, the only way out of the difficulty is to sacrifice logic for expediency, and to adopt as an arbitrary dividing line between "late-glacial" and "postglacial" some well-recognized event during deglaciation. Firbas (1939, p. 83) places the boundary at the retreat from the Fenno-scandian end moraines, which supposedly began about 10,000 years ago according to the Swedish chronology, and this convention is accepted by most workers, even though it is difficult to apply in the British Isles.

The term "late-glacial" is thus used here so

far as possible. In Firbas' region, the lowlands of central Europe, the general synchrony of retreat of two ice sheets, one to the north and the other to the south, considerably reduces the possi-

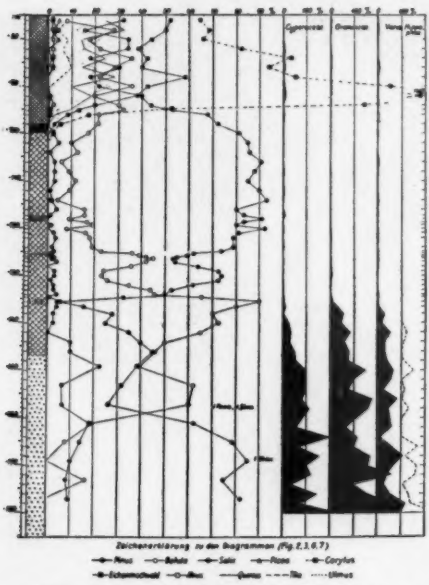


FIGURE 2.—POLLEN DIAGRAM FOR A BORING IN THE FEDERSEE IN SWABIA

Showing abundance of herbaceous pollen during late-glacial phases. From Firbas (1935, Fig. 2).

bility of misunderstanding. We cannot expect such events as the Allerød oscillation to show up everywhere in deposits of the same age, but we can expect to find that climatic conditions at this time were roughly comparable everywhere between the Alps and Scandinavia. Outside central Europe "the Late-Glacial" should not be used as a stratigraphic term, but the adjective "late-glacial" must often be used, particularly in North America, to describe that segment of time, postglacial at some locality but glacial at some other locality not far away, when the proximity of ice was a potent factor restraining biogeographic movements.

In his impressive monograph of the subject, Firbas (1935) distinguishes three phases of late-glacial age:

1. A treeless phase, corresponding to the time of the maximum of the last ice sheets
2. A subarctic phase of birch and pine woo land, in which warmth-loving trees we absent
3. A preboreal phase with the first appea ance of warmth-loving trees

The treeless (tundra) phase is characterized, n by the absence of pollen, but by large quantiti of pollen of herbaceous species (sedges, grass etc.), as conspicuously shown in Figure 2. Poll of willow, pine, and birch is represented, bu most of this is regarded as wind-borne from a distance, for the herbaceous component seldo reaches such high values (several hundred pe cent of total tree pollen) when a forest cover i present. A detailed report on this problem ha been made by Aario (1940; 1943) on the basis o a transect from the arctic tundra at Petsam into the forested region of central Finland. Th results are on the whole favorable for the belie that NBP (Nicht-Baum Pollen, nonarboreal can be used as Firbas and others have used it though there are some complications.

It is noteworthy, though perhaps to be ex pected, that the tundra vegetation of centra Europe during the late-glacial phases was of a considerably more complex type than tha found today in tundra regions. This point i emphasized in recent reviews of the problem by Godwin (1947) and Firbas (1947). Careful at tention to the herbaceous component of th pollen flora has revealed, besides the grasses sedges, *Dryas*, *Oxyria*, *Armeria*, *Empetrum*, an *Selaginella*, all of which are to be expected, such genera as *Artemisia*, *Rumex*, *Thalictrum*, *Hip pophae*, and *Helianthemum*. These genera ar central European rather than arctic in affinitie and testify to the remarkable glacial inter mingling of the biota in the region betwee the Alpine and Scandinavian ice sheets.

A map of Germany, on which are plotted th percentages of pine and birch pollen during th subarctic phase of a large number of borings (Fig. 3), makes it reasonably clear that the pin moved in from the southeast as it replaced th birch. Taking a larger view of Europe as a whole, as Firbas does (Fig. 4), it seems that th vegetational zonation during the Late-Glacial i becoming rather clear. Firbas' maps show wha a high point of elegance pollen workers have at tained in Europe; it may be churlish to re mark that there is no proof that the polle

spectra from which they are drawn are of exactly the same age.

The Postglacial.—Detailed discussion of the history of the European vegetation from the actual inception of warm conditions to the present

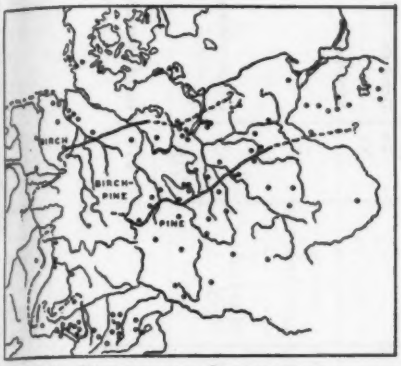


FIGURE 3.—VEGETATIONAL DEVELOPMENT DURING THE SUBARCTIC PHASE OF THE LATE-GLACIAL OF CENTRAL EUROPE

Based on pollen percentages at sites represented by vertical lines. Redrawn from Firbas (1935, Fig. 10).

seems to be unnecessary here, for the main outlines are familiar to most students of the Pleistocene, and Tables 2 and 3 embody the most important information. The account given by Zeuner (1946) is admirable, though brief; it relies heavily on the book of Karl Bertsch (1935), which has not been available to the writer. Movius (1942) gives an excellent account of the British Isles. The literature of the subject is enormous, but fortunately annual bibliographies are still being published by Erdtman in the *Förhandlingar* of the Geologiska Föreningen of Stockholm.

The large number of pollen zones recognized in postglacial sections by workers in different countries, approximate correlations of which are indicated in Tables 2 and 3, should not be allowed to obscure the main sequence of climatic changes. For most parts of Europe it is still true that three phases—the "increasing warmth", "maximum warmth", and "decreasing warmth" of von Post—are recorded in pollen diagrams and supported by a wealth of additional evidence. The widely quoted estimates of the average July temperature in Denmark (Pre-Boreal, 8° C; Boreal, 14° C; Atlantic, 16-17° C), though based primarily on marine fossils, are entirely reasonable in the light of terrestrial

FIGURE 4.—VEGETATIONAL ZONATION DURING THE CLOSING STAGES OF THE LAST GLACIATION

Closed circles: treeless glacial flora; open circles: birch- and pine-phase layers without warmth-loving trees; crosses: birch- and pine-phase layers with small but consistent amounts of warmth-loving trees. Glaciated region shaded, local glaciations not shown. From Firbas (1939, Fig. 6).

finds (Werth, 1928). On these temperature changes are superimposed the finer-scale embroideries, whether they point to a Blytt-Sernander sequence (*Boreal*, cool, dry; *Atlantic*, warm, moist; *Sub-Boreal*, cooler, drier; *Sub-Atlantic*, cooler moister) or to an even greater refinement. Some of the latter is of course phytogeographic rather than climatic in origin, as is seen in an instructive series of diagrams for beech pollen assembled by Bertsch and reproduced by Zeuner (1946, Fig. 32); beech is shown to have immigrated into southern Germany from the southeast and the southwest, and reached Swabia comparatively late. Interesting syntheses of data for pine and spruce have been prepared by Firbas (Figs. 5, 6).

Postglacial animal stratigraphy.—It is scarcely necessary to say that the stratigraphic relations of animal fossils in the Late-Glacial and Postglacial of Europe are much less well known than those of plants. The larger animals are not very

TABLE 3.—POSTGLACIAL POLLEN CHRONOLOGY FOR CERTAIN CENTRAL EUROPEAN COUNTRIES

Chiefly after Von Sarnthein (1940), with additions: Bertsch (1931); Van Campo (1947); Dubois (1947); Firbas (1934); Godwin (1943); Keller (1931/1932); Kintzler (1936); Lemée (1948); Overbeck and Schneider (1938)

FRANCE		British Zones	TYROL	FEDERSEE	RHEINPFALZ	N. German Zones	NORTHERN ITALY	HUNGARY
Plains	Mountains							
6. Terminal, culturally diversified forest; pine rises, spruce introduced			VIIIb Rise of pine	Spruce		XIb		
5. Oak-beech, fir absent	Oak, beech, fir, alder (birch)	VIII	VIIIa Upper spruce maximum	Beech-pine	Beech	XIa	*Chestnut increasing*	Beech
								Hornbeam maximum
			VII Fir-beech	Beech		Xb Xa	*Beech increasing*	*Spread of fir*
							Mixed-oak	
		VII–VIII	VI Lower spruce maximum; fir and beech begin	Mixed forest with beech rising		IX		*Oak, lime dominant; spruce maximum*
4. Mixed-oak, with less lime, more elm	Mixed-oak, lime	VII	V Hazel-mixed-oak Climatic optimum	Hazel-mixed-oak	Mixed-oak-alder	VIII	*Oak maximum*	Mixed-oak *Elm dominant*
						VII	*Hazel increasing*	

3. Hazel rises slowly	Hazel	VI	IV	Pine, with birch peaks	Pine with birch peaks; hazel and elm (sparingly)	Hazel	VI	*Fir begins* *Spruce begins*	
2. Pine	Pine	V						Pine	
1. Pine-birch	Willow-birch	IV	III	Lingering late-glacial; birch advances	Younger pine forest advancing	Pine; forest advancing	V		Pine-birch-willow *Little mixed-oak*
		III	II	Gschnitz glaciation; spruce and fir retreat	Birch advance; forest regression	Pine-birch	IV	Birch-pine	
		II	I	Buhl-Gschnitz interval; spruce, fir	Older pine		III		
		I		Buhl glaciation	Birch; forest increasing	Birch	II		
				End of Würm	Treeless tundra	Treeless tundra	I		

suitable for the purpose, and the smaller animals have been little studied. Among the few groups which have drawn a certain amount of attention, mollusks and beetles are outstanding.

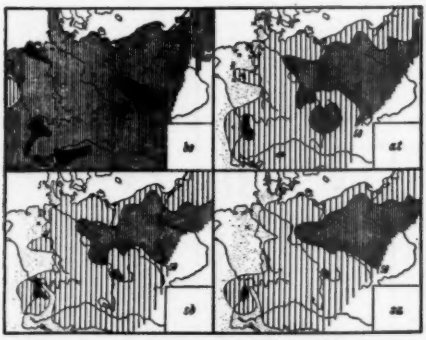


FIGURE 5.—POLLEN ISOPLETHS FOR PINE. DURING THE POSTGLACIAL

bo, Boreal; *at*, Atlantic; *sb*, Sub-Boreal; *sa*, Sub-Atlantic. Pine pollen percentages under 5, dotted; 5–50, open shading; 50–80, close shading; over 80, black. Crosses are finds of fossil wood. From Firbas (1939, Fig 4).

The picture revealed by the marine mollusks of the Baltic basin is too well known to warrant discussion here; a summary may be found in Ekman (1933b). Land and fresh-water mollusks are well represented in deposits of northern Europe as elsewhere, but no compilation like that of Baker (1920) for North America seems to be available. Among the works of more restricted scope, there is a monograph by Favre (1927) of the mollusks of the Geneva basin, in which the postglacial fossil and modern faunas are compared species by species; the postglacial specimens fall into two main faunas: one, characterized by *Goniobasis ruderatus*, implies continental, rather cool conditions, and is presumed to be of Boreal age (Favre's "Boreal", however, includes the late-glacial Magdalenian horizons); the later fauna contains a large number of Mediterranean and Pontic elements, some of which are extinct in the basin today, and is said to be of Atlantic age. No convincing stratigraphy is presented, the work having been done before the applicability of pollen analysis was generally realized by zoologists.

More satisfactory, and apparently very little known, is a remarkable work by Henriksen (1933) on the Pleistocene insects of Denmark and Scania. No less than 270 species of insects are known as Pleistocene or postglacial fossils, 240 of them beetles. This very rich material supplements at every step what is known of the plant stratigraphy, and in a few cases the occurrence of monophagous species, such as *Galerucella luteola*, enables one to predict that the food plant (elm, in this case) will eventually be found in the deposits. The proportion of aquatic to terrestrial species is naturally higher than for the fauna of Denmark as a whole, but within the peat deposits this proportion changes systematically with the relative dryness of the bog stage: the ratio varies from 50:50 in very wet *Sphagnum-Scheuchzeria* peat, to 20:80 in *Phragmites*—forest peat, and 23:77 in the driest birch-forest peat. The principal stratigraphic results are condensed in Table 4, but the Danish original, with its numerous species lists and distribution maps, is impossible to summarize in full. The catalogue gives a full account of modern distribution, fossil occurrence in Denmark and elsewhere, and general biology of each species. Of course Pleistocene beetles are known from other European countries, notably the Lower Pleistocene deposits at Boryslav in Galicia (Lomnicki, 1894), and a summary of the British occurrences, now considerably out of date, is given by Bell (1922).

The stratigraphy of the Pleistocene as established by vertebrate paleontology falls outside the scope of this review. Many of the most famous sites, important both archaeologically and biologically, cannot be dated except by their vertebrate fossils, and this procedure leads to results that are usually quite crude as well as controversial. Postglacial vertebrate remains have not lent themselves so far to a detailed stratigraphy, though it should be mentioned that Degerbøl (1933) gives a valuable catalogue of Danish mammalian finds primarily from archaeologic sites, and the Danish fishes are treated by the same author (1945).

Pleistocene Biogeography of Central Europe

General discussion.—It is convenient to begin the discussion of existing ranges and their implications with a map (Fig. 7) of the present range of *Rhododendron ponticum*, for in this case some stratigraphic information is at hand. This

species, now showing a spectacular disjunction of range and represented by different varieties in different areas, is spoken of as a "Tertiary" relict by Cain. The species may be "Tertiary", but the distribution pattern is Pleistocene. The fossil occurrences are of interglacial age (the most famous being in the Hötting breccia in the Alps, probably second interglacial), and a former widespread distribution has been dissected by repeated glaciations.

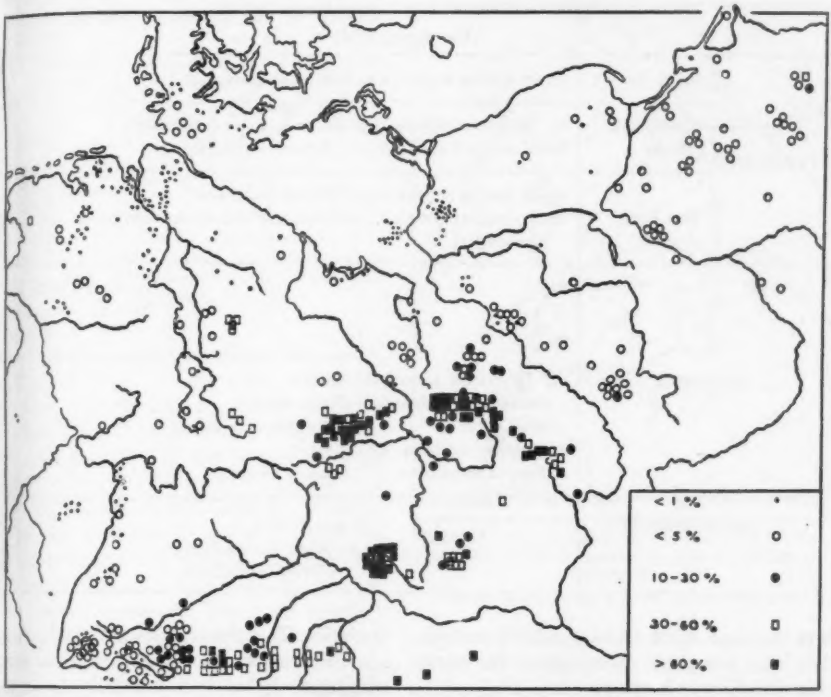


FIGURE 6.—RELATIVE POLLEN FREQUENCY OF SPRUCE DURING THE POSTGLACIAL WARMTH MAXIMUM
Redrawn from Firbas (1939, Fig 3).

Numerous cases among animals and plants could be cited to show much the same thing, though fossil evidence is not usually available. The carrion and hoodie crows (*Corvus c. corone* and *C. c. cornix*) provide a familiar example: the former is the form of western Europe, the latter that of eastern Europe, while a narrow zone of hybridization running from Italy to the Baltic Sea marks the line where the two subspecies, differentiated in isolation during a glacial stage, have met in their postglacial expansion. Another zone of overlap runs across Scotland, the hoodie crow having presumably entered Scotland directly from Scandinavia, and still another runs from the Yenisei River to the Altai Mountains and then west to the Sea of Aral. The logical assumption is that the central population of crows acquired the hoodie coloration (Huxley, 1943, p. 248–250). Other cases in which a pair of closely related species, one of eastern or northeastern and one of western or southern distribution, have come together in central Europe, are cited by Rensch (1933) (the snails *Clausilia dubia* and *C. bidentata*, the creepers *Certhia familiaris* and *C. brachydactyla*, etc.). As Reinig (1939) points out, many of the cases supposedly showing adaptive variation along a character-gradient or *cline* and interpreted in conformity with Bergmann's Rule, Allen's Rule, etc., are in reality due to postglacial changes of range. The

explanation applies even more strongly to clines that are apparently not adaptive.

In other cases, though the history of glacial and postglacial changes of range has doubtless been the same, it has not been possible to elucidate it by taxonomic studies alone—the whole of central Europe is occupied by a single wide-ranging species with no close relatives in obvious glacial refuges. In only a few animal groups (birds, mammals, certain insects, and land snails) are the systematic relations well enough understood to permit the recognition of subspecies, which are usually more illuminating in this respect than species. Among plants, where a study of chromosome numbers often makes it possible to deduce the ancestry of populations not morphologically distinct from their parent stocks, some instructive examples of Pleistocene effects have come to light. One of these is the crucifer *Biscutella laevigata* (Manton, 1934; 1937). Figure 8 shows the distribution of diploid and tetraploid races of this species; the tetraploids, which are younger than the diploids and derived from one or more of them, are vigorous and geographically aggressive and have colonized the glaciated parts of the Alps. The diploids have local, discontinuous distributions, seemingly having lost the capacity to spread, and are chiefly confined to regions known to have been ice-free during the last

TABLE 4.—SUMMARY OF DANISH FOSSIL INSECTS
(Henriksen, 1933)

Postglacial	Beech Zone	ca. 16 species appear, e.g. *Barynotus squamosus*			
	Mixed-Oak Zone	ca. 113 species appear, e.g. *Lucanus cervus* (oak insect) Some dropped out since, e.g. *Laccophilus variegatus*			
	Pine Zone	ca. 38 species appear, e.g. *Calosoma inquisitor* Some dropped out since, reintroduced with spruce plantations (e.g. *Hylobius abietis*)			
Late-Glacial				Northern Species	Cent. European Species
		ca. 75 species known, 3 extinct (e.g. *Nebria fossilis*) 15 dropped out since, e.g. *Bembidion glaciale*	Allerød	3	9
			Betula nana	6	15
			Salix polaris & *Betula nana*	9	4
			Coldest Dryas	5	1
Last Interglacial		10 species sure. e.g. *Otiorrhynchus dubius* *Pterostichus nigrita*			

glaciation. That the diploids are of interglacial age while the tetraploids are postglacial seems unquestioned; but it is doubtful whether the diploids survived the last glaciation everywhere they are now found, as Manton believes. It is more likely that the diploid races of the Rhine and Elbe valleys, at least, migrated to their present districts during late-glacial or postglacial time.

The discontinuous, "pulverized" distribution of the diploid races of *Biscutella* brings out a point that occurs with great frequency in the study of biogeography, and may be emphasized now. Other factors being equal, the rate of differentiation within the population of a species *varies inversely with the size of the population*. When the population (*i.e.*, the group all of whose members can potentially interbreed) is large, mutation to genes that are favorable under the existing environment reaches equilibrium with the forces opposing preservation of such mutations (selection, linkage with unfa-

vorable genes, etc.) at a level that yields a variable, plastic population some of whose members may be pre-adapted genetically to different environments. Large populations with a large number of (genetic) biotypes are therefore in a favorable position to spread and to undergo

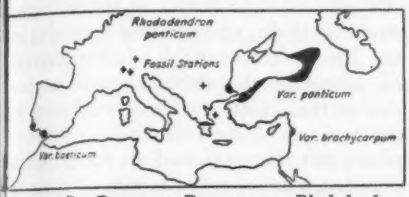


FIGURE 7.—PRESENT RANGE OF *Rhododendron ponticum*, WITH INTERGLACIAL FOSSIL LOCALITIES
From Cain (1944a, Fig 35).

rapid evolution when conditions change. In small populations, on the other hand, the dynamics of the genetic equilibrium are such that some genes, both favorable and unfavorable, are either fixed or lost in favor of their mutated alleles, and the result is likely to be a genetically homogeneous population, differing sharply from the ancestral species in characters that are not necessarily adaptive, and relatively incapable of responding in an evolutionary sense to changed environments. This is the so-called "Sewell Wright effect" or "drift", the effects of which are so conspicuous when island populations are compared with those of the mainland. From the biogeographic point of view it is correct to speak of isolation of small segments of a population as leading to "depauperization of biotypes", as does Hultén (1937). This idea has gradually come to supersede the older notion of "senility" of species. The diploid races of *Biscutella* seem to be good examples of such small populations, isolated from each other during the Pleistocene and now showing little capacity for recolonization.

Another case of plant distribution throwing some light on Pleistocene migrations can also be taken from Cain (after Waclaw, 1934). In southern Poland an outlier of the Carpathian massif has been isolated by the valley of the Dnjestr, and is now drained southward by a long series of parallel canyons tributary to that river and believed to have been cut during the last interglacial age. In the canyons themselves are two groups of plants, one (now growing in the humid forests) of western, humid-oceanic distribution, the other (now found on drier, more open hillsides) of eastern,

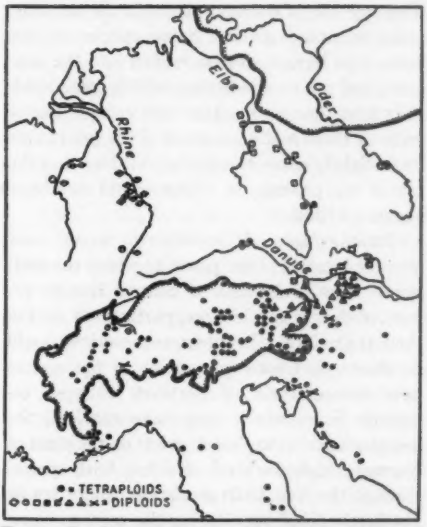


FIGURE 8.—OCCURRENCE OF DIPLOID AND TETRAPLOID RACES OF *Biscutella laevigata* IN CENTRAL EUROPE
From Cain (1944a, Fig. 56), after Manton.

continental distribution. Both groups are thought to be postglacial immigrants, the former having come during cool moist phases, the latter during the xerothermic interval. But on the interfluves is another group of plants, with no demonstrable relationship to the canyons. These are believed to be survivors of the plateau vegetation antedating the cutting of the canyons. This sort of hypothesis, according to which temperate plants stay on uplands while valleys are cut all around them by drainage arising from Pleistocene climatic regimes, does not withstand critical scrutiny. We shall have to deal with it again in the section on North America. It does not matter that in this case the Pleistocene climate under which the valleys were cut was periglacial rather than glacial. Pollen stratigraphy shows that too much has happened, in periglacial Poland as well as in regions actually covered by ice, for such an explanation to be tenable. The plants in question are cool-temperate and montane species, found

elsewhere in the Carpathians, in Siberia, and in the Caucasus. They presumably arrived in southern Poland after the birch phase and along with the pine during the subarctic or pre-boreal phases shown in Table 3 for near-by Hungary. They are not, of course, at home in the canyons, being montane species. Some species of the same type have doubtless moved into the canyons, and are now indistinguishable geographically from one of the other two groups. But if more of them had done so, or if the interfluves were slightly lower, the improbable idea that the plants are pre-canyon relicts would not have suggested itself.

Glacial refuges.—It is proper to inquire now into the location of the places to which the temperate flora and fauna of central Europe retreated during glacial ages, particularly during the last glaciation. In subsequent sections it will be shown that some proportion of the species now characteristic of northern Europe, especially Scandinavia, may have survived the last glaciation in ice-free districts on the coast of Norway, while survival of a few Irish species through the New Drift glaciation cannot yet be absolutely ruled out. During the coldest phase of late-glacial time the greater part of Europe between the Scandinavian Ice Sheet and the Alps was occupied by a "grass-sedge tundra with scattered patches of tree birches" (Godwin, 1947), so that species now at home in a biotic community of this type clearly could have survived in southern Germany, Bohemia, and Poland. Forest trees, however, are not among these species, and the whole community, though taxonomically more complex than typical tundra today (doubtless because the summers were warmer and longer at such relatively low latitudes), certainly could not have included any large fraction of the species now found in temperate Europe.

Biogeographers are rather sharply divided on the question of survival of species through a glaciation. Many workers find it impossible to believe that conditions were any more severe than today even a few miles beyond the ice border. Though they admit that districts now showing good geologic evidence of having been completely overridden by an ice sheet were stripped of their vegetation, they commonly permit their species to take refuge (in imagination) on south-facing slopes, fjords, bays, emerged continental shelves, and the like, in the immediate neighborhood of the ice. When pressed by the arguments of the opposing school, they often deny the validity of the geologic evidence, pointing to divergence of opinion among geologists, or take refuge themselves (still speaking figuratively) on the Malaspina Glacier in Alaska, where a forest is growing today. The latter, of course, is a false analogy. It is a curious fact that writers to whom it seems possible that plants "over-wintered" near or even *under* an ice sheet also find it possible to believe that plants survived the destruction of Krakatau, mantled as it was with a blanket of hot ashes 30 meters thick (Dammerman, 1948).

It will be obvious that the writer belongs to the party of opposition, which holds that such survival is unlikely for any plants not now members of the periglacial communities of Greenland, for example, and impossible for forest-tree species and their associates. It seems no longer necessary to pursue this argument by a process of assertion and counter-assertion. Stratigraphy, particularly pollen stratigraphy, is making it increasingly evident that the great ice sheets of the Pleistocene were bordered by broad belts in which periglacial climates, with solifluction phenomena and accompanying dust storms, prevailed, and that these climates were as effective barriers to the spread of warm-temperate species as were the ice sheets themselves.

Unfortunately, as research progresses, it is becoming easier to prove that a given locality was *not* an important glacial refuge, but more difficult to find a locality that was. Various workers have thought that the lower Danube valley, in Hungary and Rumania, must have served as the chief center of survival and post-glacial migration of the central European forests. Basins suitable for the retention of pollen are scarce in this region, as elsewhere in unglaciated districts, and the literature is scanty. But a few pollen diagrams are now available for Hungary, Kintzler (1936) and Soó von Bere (1940) have shown that the late-glacial pollen flora was predominantly birch and pine, as it was in southern Germany, though with somewhat higher proportions of oak and other deciduous species. (*See* Table 3, also Figure 4.) Rumanian pollen diagrams have not been seen by

the writer, but it may be that we must look as far as the Ukraine or even the Caucasus to find a genuinely important glacial refuge. On the other side of Europe, in the Iberian peninsula, there is virtually no evidence except from basins at high altitudes, while on the shores of the Mediterranean (Bate, 1928; Firbas, 1947; Blanc, 1937) the glacial-age fauna and flora were of cold-temperate or subarctic character even at sea level.

In summary, the Pleistocene glaciations have had a profound effect on the ranges of central European species. The biota in general was forced to retreat into southeastern and southwestern Europe or farther, with the result in some instances of taxonomic differentiation, and the recolonization, generally speaking, is postglacial. We should now take a closer look at the species of the Alps for further light on the problem.

Alpine biogeography.—The Darwinian view that the post-Ice Age migration of species has given rise to the boreo-alpine distribution pattern, the arctic and cold-steppe biota having moved both northward to the Arctic and upward to high altitudes in the Alps, has not been challenged except by Scharff, who doubted that there ever was an Ice Age, or if there was, that it had any important effect on biogeography. It is not worth while today to take Scharff's curious views seriously. But there have been persistent suggestions that the boreo-alpine pattern is not identical among all species showing it—*i.e.*, that some species became alpine after one glaciation, boreo-alpine after a later glaciation—, and this possibility deserves careful consideration. There are, first of all, cases where the boreo-alpine pattern is not shown by the species, but by a larger group such as a genus. A typical "species pair", one member of which is boreal, the other alpine, is shown by the midges *Diamesa lindrothi* and *D. latitarsus* (Thienemann, 1941), and several other examples are cited among Coleoptera and Hemiptera by Holdhaus (1912), such as the subgenus *Oreostiba* of the staphylinid genus *Atheta*, six species of which are strictly boreal in Europe, while four others are alpine. Such cases suggest multiple glaciation, one glaciation to push the group into central Europe, a second permitting the specific differentiation of alpine from boreal forms. In view of the wide variation in rate of evolution among organisms, however, it would be naive to assume that all such cases *necessarily* imply multiple glaciation.

It is worth noticing that several of the bird species of boreo-alpine distribution (redpoll, ring-ouzel, ptarmigan, etc.) are represented in the Alps by different subspecies (Reiser and Holdhaus, 1935), and the same is certainly true of mammals. This suggests that the degree of taxonomic differentiation is as much a function of how closely one looks at a species as of the age of its isolation.

Again, it is a familiar fact that sibling species often occur together within a very small area. Jeannel (1928) cites several pairs of closely related species in the beetle genus *Trechus* in the Carpathians and mentions that no less than four sibling species (the group of *T. strigipennis*) occur together in the alpine zone of Mont Rose in the Alps. Such species must have differentiated in different places or at different times or both; but as it is unlikely that four *different places* were available in the neighborhood of Mont Rose the implication is that the same places served during *different glaciations* as regions of isolation.

Coleopterists seem to have been especially active in urging the view that the alpine species are not all of the same age. Holdhaus (1932, 1933a, 1933b, 1939; Holdhaus and Lindroth, 1939) has perhaps been the leader, but the French logic of Sainte-Claire Deville forms a more attractive starting point for discussion.

According to Sainte-Claire Deville (1928), the Darwinian position among coleopterists is represented by the views of Oswald Heer. But the number of species to which Heer's explanation applies—*i.e.* typically boreo-alpine species with no close relatives in central Europe—is very small, perhaps half a dozen among the more than 5000 alpine species. Instead, one finds facts such as the following: (1) The largely arctic staphylinid genus *Mannerheimia* is represented in central Europe by four species; *M. arctica*, which lives in Siberia and extreme northern Europe, occurs also in the Col du Stelvio; *M. aprutiana* is isolated in the Abbruzzi at Cime de la Majella; *M. doderoi* is similarly isolated at Valsa Varanche; and *M. divergens* is known only from Siberia, Jamtland in Sweden,

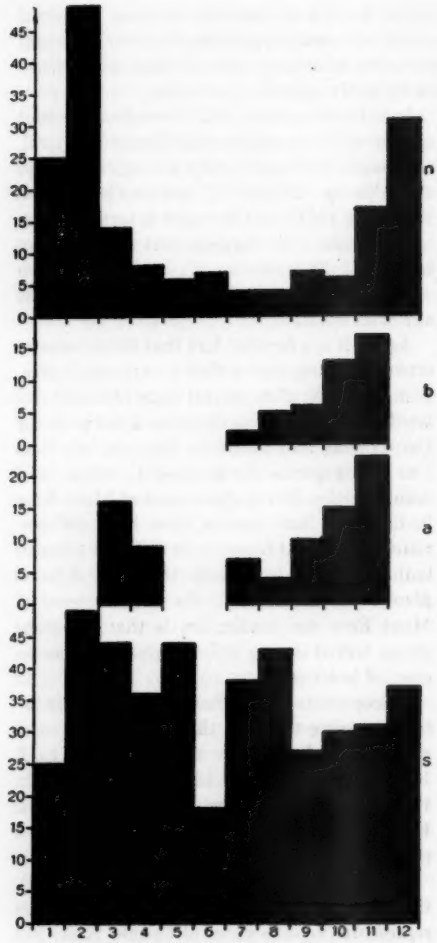


FIGURE 9.—FREQUENCY DISTRIBUTION OF ENDEMIC BEETLES IN CERTAIN GENERA, ACCORDING TO SMALL REGIONS IN THE ALPS

n, a northern transect from west to east; *s*, a southern transect; *b* and *a*, intermediate transects. Ordinate: number of species. From Heberdey (1933, Fig. 12).

and the Altai Mountains. This is a relict distribution much older than Heer's hypothesis would permit. (2) *Hypnoidus hyperboreus* is distributed across northern Europe from Norwegian Finnmark to the Yenisei River; it then occurs in a number of isolated localities on the southern flank of the Alps, such as the Dolomites, Mont Rose, Haute-Maurienne and Mont-Cenis, and the Provençal Alps. Why, if Heer was right about glacial-age intermingling of faunas in northern Europe, are there no relicts on the northern flank? (3) *Dytiscus lapponicus* has its southern limit of continuous northern distribution at Amsterdam; there is a representative race, *disjunctus*, in the region of the Lago della Maddelena, but the typical race also occurs in the Alps (La Grave, Mont-Cenis, Simplon). This certainly suggests that *D. l. disjunctus* is a "preglacial", *i.e.*, interglacial relict. (4) The coleopteran fauna that *has* colonized the glaciated Alps is the "Hercynian" fauna, *i.e.*, the one composed of widely distributed central European species, occurring also in the Vosges, the Jura, and the south German ranges. The peculiar species, those whose distinctness and spotty distribution suggest that they are relicts of an earlier fauna, are largely confined to the "massifs de refuge", the plateau remnants of the southwestern and southeastern parts of the Alps (a few also occurring on the north flank), which were not glaciated at least during the last glacial age.

The term "massif de refuge" goes back to the botanists, Chodat and Pampanini. It is widely used in studies of this problem. A massif de refuge is not a nunatak, since it was not completely surrounded by ice. There seems to be no question that such areas exist, or that they now shelter a number of peculiar species. It is also true that the endemic species are not only isolated from each other but are divisible into two groups, the southeastern and the southwestern parts of the Alps having completely different faunas, and being separated by a (formerly glaciated) zone now colonized by widely distributed species. As to the age of the distribution of the endemics, however, there is controversy. Some authors believe them to be "preglacial" relicts (Holdhaus), while others maintain that though the species may antedate the last glaciation their present distribution is postglacial (Heberdey). Heberdey's analysis (1933) is worthy of some attention, as it is based on a thorough statistical analysis of the alpine Coleoptera. It is, first, restricted to genuinely alpicolous species occurring above 1200 meters, which do not eat phanerogamous plants and so are not tied to them in migration, which are flightless

or capable of spreading with great difficulty, and which belong to genera or subgenera having at least five species in the Alps, so that line was depressed below the level of their lowest occurrence today. They must therefore have reached their present localities postglacially. If

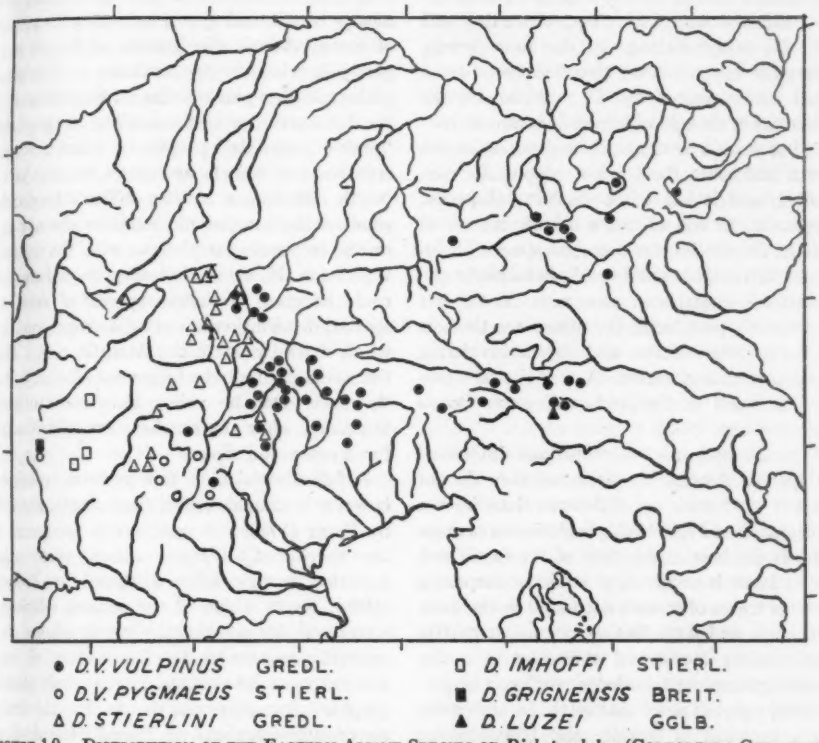


FIGURE 10.—DISTRIBUTION OF THE EASTERN ALPINE SPECIES OF *Dichotrachelus* (COLEOPTERA, CURCULIONIDAE) Redrawn from Franz (1936a, Abb. 6).

close relatives can be compared. By dividing the beetles further into widespread versus endemic species, and plotting the numbers of endemics in these genera by geographic districts, bimodal frequency distributions are shown to be real (Fig. 9). An east-west transect along the northern flank of the Alps (*n*) makes it clear that the endemics are almost completely separated by a central zone of widespread species, and this pattern is still more obvious on parallel transects farther south, until the south flank (*s*) is reached, where it breaks up. But these endemics, though they were clearly differentiated during a glacial age, cannot have survived a glaciation on the north flank of the Alps, for we know that the Pleistocene snow this is true for the north flank, there is no reason to suppose it is not true for *massifs de refuge* elsewhere.

It is possible, of course to argue, that Heberdey's treatment of the problem is overly synthetic, in that it conceals under the term "endemic" real differences in age of species. Accordingly, it is not likely to be accepted by workers who consider, on the basis of detailed studies of smaller groups, that traces of multiple glaciation are still detectible in the fauna of the Alps. Franz (1936a) presents an argument which, though not irrefutable, is typical of the sort of evidence biogeographic studies can yield. Figure 10 shows the distribution, in the eastern Alps, of the species of the curculionid genus *Dicho-*

trachelus. Evidently three stages of faunistic differentiation are represented. *D. luzei* and *D. grignensis* are extremely local endemics, each supposedly having survived the last glacial age on a different *massif de refuge*, where they still are. *D. imhoffi* belongs to the same group, though it has colonized glaciated areas somewhat more successfully. *D. vulpinus*, on the other hand, though widespread, is almost confined to *massifs de refuge*, its disjunction on the north and south flank is not edaphically controlled, and it has left a distinct subspecies, *pygmaeus*, in one of the southern centers of refuge. *D. stierlini*, the youngest species phylogenetically, occurs indifferently in formerly glaciated and unglaciated mountains. As the last is obviously postglacial, the others are thought to imply differentiation and disjunction dating from an earlier glaciation. A very similar situation is found in the land snail genus *Orcula* (Zimmerman, 1932).

Though such cases establish age differences in specific distribution patterns, they do not require that each age difference date from a different glacial age. Multiple glaciation perhaps affords the best explanation of the facts, and, as we know it occurred, it would be surprising if some traces of it were not found in the modern fauna and flora. But so long as alternative explanations (accidental spreading to a distance, incomplete knowledge, etc.) can be presented, rigorous proof that might be acceptable to a geologist is lacking, and biogeographic data remain far inferior to stratigraphic information as indicators of multiple glaciation. We can summarize the discussion, then, by saying (1) the colonization of glaciated districts within the Alps is postglacial; (2) the species driven from the Alps and from northern Europe by glaciation survived the glaciation somewhere; (3) the principal refuges were in southwestern and southeastern Europe; (4) some detailed distributional studies suggest that alpine distributions are not all of one age, and may reflect multiple glaciation.

Relicts of xerothermic intervals.—As the postglacial stratigraphy shows, the climate of central Europe has been warmer and drier than today. During such intervals some species have expanded their range from the east, and some of them have contracted once more (*see* map for pine, Fig. 5), while others have had their range greatly dissected by subsequent climatic changes.

Species of interest in this connection are mostly continental types, belonging to genera of central Asiatic distribution, and some now persist in relatively dry localities, such as sand plains and open pine woodlands. In other words, the distribution pattern is a mirror image of the "prairie peninsula" pattern of eastern North America and reflects analogous causes. As in North America, it is often difficult to decide whether the xerothermic localities are natural or due to human interference with the natural vegetation. However that may be, a long list could be given of eastern species of very restricted distribution in central Europe, some of which extend even to the Atlantic coast. The list would naturally be longer for Hungary and the lower Danube valley than for southern Germany, while the numbers are still smaller for France and Spain.

A full discussion of this problem, confined however to animals rather than plants, is given by Franz (1936b). A particularly good case is the katydid *Ephippigera vitium*, whose distribution is thoroughly analyzed by Zeuner (1929). As to which of the several relatively warm and dry postglacial climatic phases was primarily responsible for this leakage of continental types into central Europe, only stratigraphic information can decide. For the truly continental organisms, the Boreal interval offers the most reasonable guess; for some that require warm but not necessarily dry conditions the Atlantic phase was doubtless responsible. But only in a few cases, such as that of *Naias flexilis*, which is known to be a Boreal relict (Sandegren, 1931/1932), is it possible to be certain on this point.

Scandinavia.—In central Europe, as we have seen, the "glacial refuges" are not likely to have harbored warm-temperate species or species that are widely distributed in the region today. Climatic conditions were too cold in the Danube valley, for example, to permit the persistence of any large fraction of the members of the mixed-oak forest community, and the species that did persist there are those now found chiefly in arctic and subarctic regions. When we reach Scandinavia, however, the problem of

Pleistocene biogeography begins to wear a different aspect. Much of Scandinavia is subarctic today and its biota, particularly in the mountains, is markedly impoverished. The probability increases, therefore, that species now found in the region may have survived glaciation somewhere in the near vicinity. At any rate, fairly extensive survival during the last glacial age is accepted by most students of the problem, including some (such as Faegri) who have had first-hand experience in pollen stratigraphy. Faegri's review (1937) of the problem may be consulted for references to the important literature, while a more recent account is given by Dahl (1946).

Many of the alpine plants of Scandinavia are widespread, occurring wherever the mountains are high enough, e.g. *Salix herbacea*. It is not possible to infer very much from the distribution of this group; many of them doubtless survived the last glaciation in the immediate neighborhood of the ice, for they are plants that live in Greenland today, but their distribution is so general that no particular refuge or group of refuges can be pointed to as any more probable than another. These plants must be left out of the discussion. There is, however, another group, the so-called "rare" alpine plants, which are much more localized, and some of them show rather remarkable disjunctions. Generally, as was shown in convincing fashion by Nordhagen among others, these species center around districts, especially on the southwestern and northwestern coasts of Norway, which were not covered by ice during the last glacial age, and are absent from the central region. These glacial refuges must have been of the character of nunataks, for ice-free areas are not likely to have persisted at sea level along the present coast, but nunatak survival is a definite possibility for some of the plants.

Certain species and species groups apparently have undergone some taxonomic differentiation owing to their isolation in several distinct refuges. *Papaver* (a poppy) and *Arenaria* (sandwort) are in this category. On the other hand, certain plants seem to have shown great taxonomic conservatism: the *Poa laxa* group, for example, contains forms that are almost indistinguishable in Scandinavia, Scotland, and Iceland, and that are distinguishable with difficulty from *Poa laxa* in the Alps, *P. Nyradiana* in Transylvania, and *P. Fernaldiana* in North America. The distribution, both wide and spectacularly disjunct, evidently antedates the last glaciation. If so, it is remarkable that there has been so little divergence among the Icelandic, Scandinavian, and Scottish populations. However, the possibility that all the latter may have survived together in northern Europe and reached their present stations postglacially does not seem to have been adequately excluded.

It is possible, of course, to question the whole set of assumptions underlying the conclusions of the Scandinavian botanists. Disjunctions of a few miles or even several hundred miles in the ranges of alpine species do not *require* glacial survival for their explanation. Some cases may be accidents of the sort involved in the colonization of oceanic islands. Others may be relicts of a wider range in late-glacial time, dissected subsequently: first by warming at the time of the climatic optimum, and later by the swing to oceanic conditions that seems to have been the latest major climatic change in northern Europe (the "Sub-Atlantic" of the Blytt-Sernander scheme). The apparent association of the rare alpine plants with less completely glaciated districts may be fortuitous. The fact remains that, if there were glacial refuges along the coast of Norway, the plants in question are such that an appreciable fraction could have survived glaciation there.

Similar considerations doubtless apply to the beetles which, according to Lindroth, must also have been "Würmüberwinterer" in Scandinavia. These are, first (Lindroth, 1935), the 15 species of boreo-British distribution, lacking in northern Europe south of the Baltic, and second (Lindroth, 1939), some 92 species or about 29 per cent of the Scandinavian Carabidae. Of the latter, most or all are found near or in the supposed glacial refuges and are absent from central Scandinavia. The case is admittedly strong for glacial survival of the alpine species, just as it is for the plants. But it is not clear in many cases why postglacial immigration is excluded, for some are winged forms, and, when we learn that the list includes some forest forms and at least two carabids of strictly sea-coast distribution that could easily be transported across salt

water, the evidence seems decidedly weak. We are left, then, with a strong inherent possibility of glacial-age survival on the part of a fairly large component of the Scandinavian flora and fauna, and no convincing proof of it.

The British Isles

The problem.—One of the most popular topics in all biogeography is the question whether the whole of the fauna and flora of the British Isles immigrated in postglacial times, or whether some fraction survived from an earlier time. The attractiveness of this problem arises in part from its manageability. For a given taxonomic group the British list is always small in comparison to that of the mainland, British distributions are often exceedingly well known owing to the inexhaustible supply of amateur and professional naturalists, and the most elementary comparison between British and French lists produces at once some fascinating problems. As a result, the literature is enormous and it is difficult to achieve a balanced presentation. The problem is complicated by the question of the relations of land and sea during the Pleistocene, for these are by no means clear.

Though much could be written about biogeographic connections between Britain and the Continent throughout the Pleistocene, some of the most important fossiliferous beds are of such controversial stratigraphic position that it is not profitable in this review to go back to early and middle Pleistocene times. Heim de Balsac (1930) may be consulted for an absorbing brief account of the Pleistocene history of British land mammals, particularly the small ones that are often more instructive because they are much commoner as fossils. It seems best to begin with the last glaciation, and here Movius (1942) has proved an invaluable guide. The essential facts, some of which are unfortunately subject to change without notice, are as follows:

Stratigraphy.—1. The Upper Chalky Boulder Clay and its equivalents, regarded as of Warthe (Würm I) age, date from the first part of the last glaciation, which covered Ireland and left only a small part of southern England unglaciated. At the climax of this glaciation the British Isles were firmly attached to the Continent, and Ireland was joined to England, but it is doubtful that any animals less hardy than polar bears were able to cross into Ireland.

2. The succeeding subage, the "Aurignacian" oscillation, was a warm one, almost as well marked as the "E" interglacial, as shown by data summarized in Table 1. (Unfortunately the possibility remains that some of the deposits placed here by Movius and others really belong to the "E" interglacial (Gams, 1938)). During part of this interval the March-Nar submergence took place, and England may have been cut off from direct connection with the Continent just when land connection would have been most effective for migration of the biota.

3. The New Drift (Hunstanton-Hessle) glaciation, which followed, is regarded as of Brandenburg (Weichsel, Würm II?) age and was severe, though not so extensive as the preceding. It is a matter for debate whether conditions in England and Ireland beyond the limits of this glaciation were so rigorous as to extinguish the characteristic biota. In other words, the question is not one of "preglacial" distribution, but of survival from the Warthe-Brandenburg interval. It is conceded that at some glacial maximum the land mass of Ireland was more extensive than today; the difference in sea level is put at 50 fathoms (91 meters) by Charlesworth (1930), a figure that permits fairly considerable addition to the dry land of southern Ireland. Survival of some nonarctic plants and animals on this emerged continental shelf is regarded by Charlesworth as "just possible".

4. Subsequent to the New Drift glaciation there is evidence of two halts or readvances of the ice margins in Great Britain and Ireland, the "Scottish Readvance" and the "Valley Glaciation". These are probably to be correlated with the Pomeranian and Fennoscandian end moraines, respectively. The intervening times (First Retreat—Daniglacial and Second Retreat—Gotiglacial) were periods of severe though ameliorating climate, to judge from fossiliferous deposits assigned to them. These deposits are not found, however, in extreme southwestern England and Ireland, and it is not known whether conditions in those areas precluded the survival of warmth-loving species.

5. A "land bridge" between England and the

Continent, certainly present during glacial ages, equally certainly persisted until the Boreal phase (Godwin's pollen zones IV and V), for peat and forest remains of this age (the "moorlog") have been found *in situ* on the Dogger Bank in depths as great as 27 fathoms (50 meters). Evidently (for a detailed summary of evidence *see* Godwin, 1943) the major rise of sea level came rather suddenly, in pre-Boreal and Boreal times, and was eustatic. Subsequently the British Isles have shared in the crustal upwarping of northern Europe, and in some districts this upward movement of the land is still going on. It is not so clear whether there was a contemporary land bridge from England to Ireland. Evidence on this crucial point is difficult to obtain, owing to post-submergence modification of the Irish Sea bottom (Charlesworth, 1930). If the present sea level were lowered by 40 meters, in an attempt to restore the pre-Boreal level, Ireland would still be an island, though its shores would approach those of Great Britain much more closely than they do now. A greater lowering of sea level, of the order of 100 meters (Farrington, 1945, argues for 120 meters as a minimum figure), would provide the desired bridge, but so low a level is not likely to have existed since the last glacial maximum, when few animals and plants could have used the bridge. It has sometimes been argued that cold-steppe forms such as the mammoth could have crossed to Ireland over a bridge of sea ice.

The beetles.—The biota of Great Britain and Ireland, though somewhat impoverished owing to its peripheral situation, is definitely not disharmonic; there are many gaps, but all the principal ecologic niches are filled, usually by forms identical with those found on the Continent, sometimes by closely related but distinct species. In other words the British Isles are typical "continental" islands in the biogeographic as well as in the geologic sense.

Most of the problems of British biogeography are lucidly set forth in Sainte-Claire Deville's analysis (1930) of the Coleoptera, which serves accordingly for an introduction to the subject. Sainte-Claire Deville begins with a theory, perhaps "un peu simpliste", attributed to W. E. Sharp. According to this survey, there are three groups of British beetles:

1. The "arctic", "glacial", or "celtic" element, found in the Scottish Highlands, Ireland, and in England as far south as the Pennines or even Dartmoor.

2. Widely distributed forms, more abundant in England than in Scotland or Ireland.

3. A not very homogeneous group, containing species isolated and local in southern England, some members of which are found in southwestern Ireland, but not in Scotland. Its western members (otherwise distributed along the Atlantic coast south to the Iberian peninsula, and sometimes showing an Iberian-Irish disjunct distribution) are called "Iberian" or Lusitanian", its eastern members "Teutonic".

Invasion of groups is postulated in the order named, with the break in continuous connection between Scotland and Ireland having occurred between the arrival of Groups 1 and 2.

The author then proceeds to his own analysis. We have the following groups:

A. A group of continental, heath- or open-country forms, extending out of the central Asiatic land mass, a few, such as *Nebria livida* (Fig. 11A) reaching England, but rare or local there. *None are found in Ireland.* About 3 or 4 per cent of the British Coleoptera belong to this group, whose presence seems to indicate that the formation of the English Channel postdates a phase of open country and antedates a phase of continuous forests.

B. The "boreo-British" group (Fig. 11B). These are not only extremely localized in Britain, as if relicts, but some seem to have diverged somewhat in physiological requirements, tolerating more warmth than do the related populations in Scandinavia. (The latter situation is very familiar in the case of the Irish hare, *Lepus hibernicus*, most closely related to the Alpine form, but ranging to sea level in Ireland. It is generally considered that absence of competition with the common hare, *L. europaeus*, has permitted this diversification. Steinböck, 1942, points out that several of the famous arctic-alpine fresh-water animals, such as the crustacean *Branchinecta paludosa* and the turbellarians *Otomesostoma auditivum* and *Planaria alpina*, though behaving as cold-water stenotherms in the Alps, are by no means so in the Arctic.) Some antiquity is implied for the boreo-British Coleoptera both by their isolation

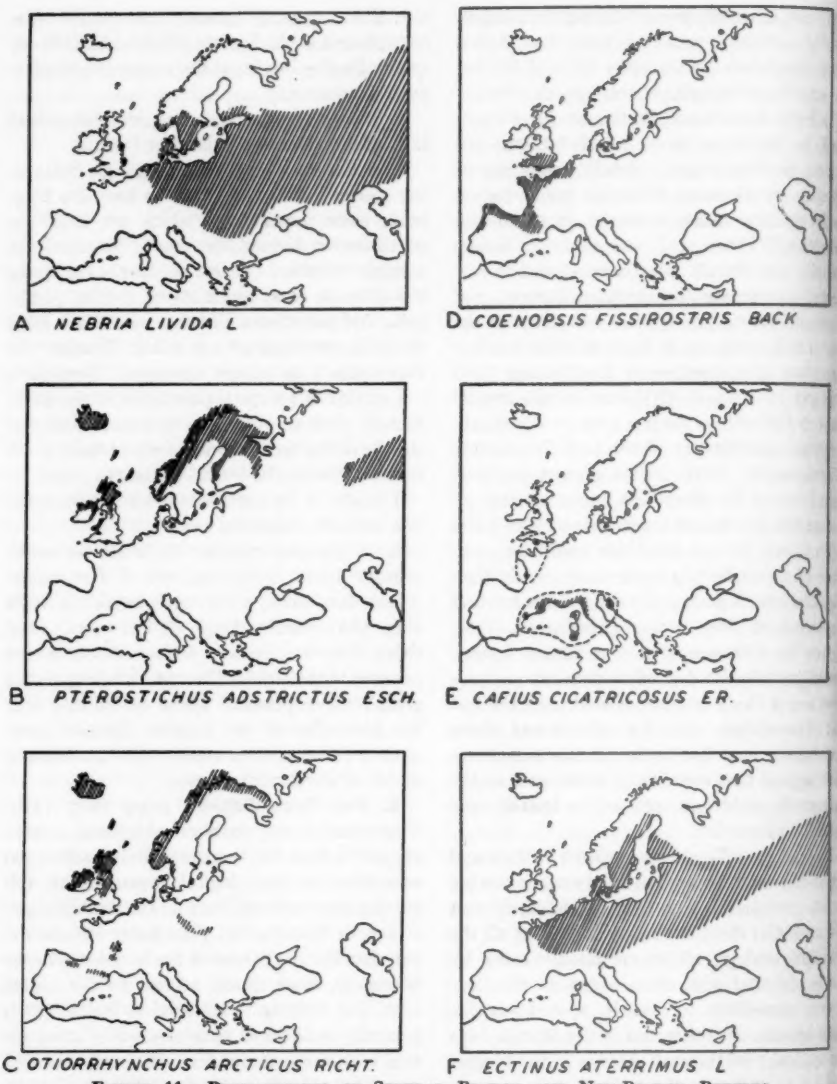

A NEBRIA LIVIDA L
D COENOPSIS FISSIROSTRIS BACK
B PTEROSTICHUS ADSTRICTUS ESCH.
E CAFIUS CICATRICOSUS ER.
C OTIORRHYNCHUS ARCTICUS RICHT.
F ECTINUS ATERRIMUS L

FIGURE 11.—DISTRIBUTIONS OF SEVERAL BRITISH AND NON-BRITISH BEETLES

Redrawn from Sainte-Claire Deville (1930). *A*, an open country species; *B*, boreo-British; *C*, boreo-alpine; *D*, *E*, Lusitanian; *F*, non-British.

and by their divergence, though we may discount Sainte-Claire Deville's suggestion that they lived on a hypothetical North Atlantic continent before its dismemberment.

C. The familiar boreo-alpine species. This is a more numerous group than the last, containing about 75 species, 34 in Ireland. Figure 11C gives a famous example.

D. A very numerous group of species whose distribution outside Britain includes the Mediterranean islands or North Africa or both. It can be subdivided into those fairly eurytherma

species that also occur as far north as Denmark, and those unknown north of Latitude 50°N. except in the British Isles.

E. An almost equally numerous group of common European species, which do not extend beyond the north shore of the Mediterranean. They can be subdivided as is Group D, and then we find that the second subdivision contains the celebrated Lusitanian element, some members of which are fairly evenly distributed (Fig. 11D), while others show more or less disjunction (Fig. 11E).

These are the main distribution patterns found among the British Coleoptera, and, with the addition of the "American" element, to be discussed below, other taxonomic groups present almost identical categories. This is not the whole story, however, for there is another group of beetles that are not British but look as though they ought to be. It is always dangerous to argue from lacunae, but about 200 species, *i.e.*, some 6 per cent of the British list and 5 per cent of the French list, reach the Channel on a broad front but are lacking in Britain (Fig. 11F). A remarkable example from another group is the bat *Myotis myosotis* (Barrett-Hamilton, *in* Barrett-Hamilton and Hinton, 1910–1921, Part IV, p. 191), which is one of the commonest European bats today, as it apparently was during the last interglacial age, and moreover is migratory. About half this number form a homogeneous group of forest species, which seem to have accompanied beech forests in their postglacial spread, but unlike the beech were unable to cross a water barrier; most of them are absent from all the European insular faunas with a few exceptions in insular Denmark.

Certainly the majority of these facts are fully in accord with a hypothesis of postglacial dispersal from Europe to the British Isles. Some of them fit in extremely well with what is known of the postglacial stratigraphy. The boreo-British and boreo-alpine species evidently followed rather closely on the retreat of the ice in the classic Darwinian manner, and while it is quite possible, as Lindroth (1935) maintains, that the former pattern is of Würm date while the latter reflects both Riss and Würm glaciations, proof is lacking, and both groups may be of the same age. Boreo-British species may be those not pushed far enough south during the last glaciation to be drawn into the zone of retreat of the Alpine ice sheet. It should not be forgotten that the mountains of Britain and Scandinavia are much more oceanic than those of central Europe, and that not all boreo-British species could be expected to be boreo-alpine. Group A above implies a spread of open-country forms across a dry English Channel to England but not to Ireland in pre-Boreal time. In Boreal and later times those warmth-loving forms that could use the land bridge or were able to jump across the Channel did so (Groups D and E), while others did not; and the latest wave of migration, accompanying the spread of beech forests, largely failed to cross the Channel which had by then come into existence.

Land bridges.—A noteworthy case bearing on the existence of the land bridge in Boreal time and its severance later is presented by Ullyott (1936). The presence of the turbellarian *Polycelis cornuta* in England, and the absence of *Planaria gonocephala*, imply rather definitely that the separation of England took place after the stream temperatures reached 12° C., but before they reached 16° C. This deduction, based on the temperature range tolerated by *P. cornuta* and on the extreme improbability that fresh-water flatworms would cross salt water, might be extended: one might say that the absence of *P. cornuta* from Ireland shows that the separation of that island took place before the stream temperatures rose to 12° C. Unfortunately for this argument, *P. cornuta* is also absent from Scandinavia, which was surely connected with Denmark during the Boreal phase (Jessen, 1935). Thus turbellarians do not always migrate where they are supposed to, and negative evidence must be used with extreme caution.

Another very interesting situation is not adequately discussed in the literature, but has been called to the writer's attention by G. E. Hutchinson. It has to do with the British land mammal fauna, summarized in Table 5. We may take first the Isle of Man, situated in the Irish Sea and broadly joined to England by a shelf less than 40 meters in depth, but separated from Ireland by deep water. Its mammalian fauna is nevertheless distinctively Irish:

TABLE 5.—SYNOPSIS OF THE SMALLER BRITISH LAND MAMMALS
Compiled by G. E. Hutchinson from various sources

Species or Species-Group	Ireland	Man	Shetlands	Orkneys	Hebrides (Inner, Outer)	Guernsey	Jersey	Great Britain and elsewhere
Crocidura russula * (1)	absent	absent	absent	absent	absent	*russula*	*russula*	*cassiteridum* in Scillies; widespread in Europe
Sorex araneus 3	absent	absent	absent	absent	absent, Outer; *granti* on Islay	absent	*fretalis*	widespread
S. minutus	present	present	? absent	present	present	absent	absent	widespread
Neomys fodiens	absent	absent	absent	absent	absent, except Skye	absent	absent	widespread
Erinaceus europaeus 1	present	present	introduced	introduced	Mull, Bute	? present introduced	? present introduced	widespread
Talpa europaea 4	absent	absent	absent	absent	Mull (? introduced) Bute	absent (on Alderney)	present	widespread
Lepus timidus 1	*hibernicus*	absent	absent	probably extinct, reintroduced	probably extinct, reintroduced	absent	absent	*scoticus* in Scotland
L. europaeus 4	absent	probably introduced	absent	absent	absent	absent	absent	common in England
Muscardinus avellanarius 4	absent	absent	absent	absent	absent	absent	absent	southern Great Britain
Micromys minutus 4	absent	absent	absent	absent	absent	absent	absent	southern Great Britain
Apodemus sylvaticus 1	present	present	*fridariensis*, etc.		*hebridensis*, etc.	present	present	abundant
A. flavicollis 4	absent	absent	absent	absent	absent	absent	absent	southern Great Britain
Arvicola amphibius 4	absent	absent	absent	absent	absent	absent	?	common
Microtus agrestis 3	absent	absent	absent	absent	subspecies	absent	absent	common
M. arvalis 2	absent	absent	absent	*orcadensis* (5 subspecies)	absent	*sarnius*	absent	absent; common on Continent
Clethrionomys glareolus 3	absent	absent	absent	absent	Raasay (subspecies)	absent	*caesarius*	common; *skomerensis* on Skomer
Mustela erminea 1; 2–3 (double invasion)	*hibernica*	*hibernica*	absent	absent	*ricinae* (feebly differentiated), Jura, Islay	present	present ? subsp.	present; Scotch form smaller
M. nivalis 4	absent	absent	absent	absent	absent	absent	absent	common

the list, given in an inaccessible note by P. M. C. Kermode (1917), includes *Pipistrellus pipistrellus*, *Plecotus auritus*, *Erinaceus europaeus*, *Sorex minutus*, *Orytolagus cuniculus*, *Lepus europaeus* (both the latter introduced), *Apodemus sylvaticus sylvaticus*, the introduced rats and mice, and *Mustela hibernicus*. Thus no land mammal lacking from Ireland occurs on Man except the introduced common hare; the typical species that are restricted to England and Scotland (such as the mole, *Talpa europaea*, the common shrew, *Sorex araneus*, and all the Microtinae) are also absent from Man; while the occurrence of the very distinct Irish species (or subspecies) of stoat, *Mustela hibernicus*, adds positive support to the abundant negative evidence for Irish affinity. These facts certainly suggest that Man received its mammals when England and Ireland had the same fauna, and that the land connection between England and Man was broken before the separation of England from the Continent. A land bridge between Man and Ireland in postglacial time is improbable, and is not required by the data; but there is some geologic reason to accept the idea of earlier separation of Man from England. At present the depth of water between Man and England is about the same as in the English Channel, about 40 meters, and this is the approximate amount of the post-Boreal submergence that drowned the "moorlog" in the North Sea. But it is entirely possible that the land has risen farther above the (also rising) sea in the region of Man than it has in the neighborhood of the Channel. Man lies *inside* the zero isobase for a postglacial emerged shore line, the so-called "25-foot beach", which has been referred to as the "Littorina shoreline" (Movius, 1942), though Godwin (1943) is more cautious. Possibly, of course, the Irish stoat has done some island-hopping, in which case the whole interesting story breaks down.

It is also fairly clear from Table 5 that Guernsey has preserved relicts of a pre-English mammal fauna. One of these is a *Microtus* of the *arvalis* group, represented in Britain only by the various *orcadensis* forms from the Orkneys, though known as a fossil (*M. corneri*) from the Ightham Fissure (? Middle Pleistocene); the other is the continental shrew, *Crocidura russula*. The presence of these animals, and the absence of *Sorex araneus*, *Talpa europaea*, the hares, the dormouse, and *Apodemus flavicollis* imply that Guernsey was separated from France before England was. This is just possible, though the present depth of water is about the same. Yet it is difficult to know how seriously to take this evidence, since Jersey, whose separation must have been very recent, has a bank vole, *Clethrionomys caesarius*, a supposed descendent of the Ightham *C. kennardi* and one of the insular representatives of *C. "nageri"*; the others are found on Skomer off the Welsh coast and Raasay in the Hebrides. Jersey also has an endemic subspecies of *Sorex araneus*, and the native stoat, though little known, is probably to be distinguished subspecifically from that of the mainland.

The presence of a *Crocidura* in the Scilly Islands (Hinton, 1924) is most remarkable. This is the only British *Crocidura*, living or fossil. A depression of sea level by approximately 80 meters would be necessary to join the Scilly Islands to the mainland, so that if this shrew was a postglacial immigrant it must have been a very early one, *i.e.*, pre-Boreal. Of all the British mammals, this shrew is least likely to have crossed to an island over water, so it is probably safe to argue from its presence that some southern species reached Britain very early and have been isolated subsequently by climatic changes postdating the climatic optimum.

The most uncomfortable problem is presented by the Outer Hebrides, which have an endemic subspecies of the *Microtus agrestis* group. It would seem that representatives of *Microtus arvalis* were the first voles to reach England, and that they spread all over Great Britain as far as the Orkneys, but not to the Shetlands or to Ireland. The absence, or rather the peripheral distribution (*orcadensis*), of the *arvalis* group in Great Britain must then be the result of competition with the later wave of *agrestis* forms; it should be noted that no small island has more than one species of vole. But the distribution also implies that the Outer Hebrides were joined to Great Britain until after the separation of Ireland, and this seems impossible, in view of the very deep water now separating the Outer from the Inner Hebrides.

In summary, the strictly zoogeographic inter-

pretation of the colonization of Britain by mammals, as communicated by Professor Hutchinson, is as follows:

1. Free passage to Ireland, Man, the Shetlands, and the Orkneys, of *Sorex minutus* and *Apodemus sylvaticus; Mustela hibernica* or its precursor reached Ireland and Man, but did not go as far north as the Shetlands. *Erinaceus, Lepus timidus* subsp., and some larger animals reached Ireland; but no voles were in this wave. *Crocidura cassiteridum* or its ancestor was living on emerged land in the English Channel, but not far enough north to reach any other region now dry except the Scilly Islands.

2. Passage to Ireland, Man, and Shetlands interrupted. Entry of voles of the *M. arvalis* group. *Mustela erminea* of ordinary type reached at least as far north as Guernsey.

3. Entry at least of *Microtus agrestis* and *Clethrionomys glareolus* after separation of Orkneys and Guernsey but before separation of coastal islands of Great Britain, including the Outer Hebrides, and of *Sorex araneus* after separation of the latter.

4. Entry of noninsular modern inhabitants of Great Britain: mainly southern species, such as *Muscardinus, Micromys, Lepus europaeus*, but some quite widespread, as *Mustela nivalis*.

This is the "naive" or nongeologic interpretation, as Professor Hutchinson has emphasized, but except for the problem of the Outer Hebrides it agrees reasonably well with the stratigraphic evidence, and suggests areas (Jersey, Guernsey, Man, etc.) where sea-level changes should be investigated by other means.

Glacial survival and the Lusitanian problem.—So far we have discussed postglacial immigration only, and certainly the great majority of British plants and animals have entered the islands since deglaciation. A few facts, however, although perhaps magnified in the minds of biogeographers through constant reiteration, seem to point to the survival of some appreciable fraction of the British biota through at least one glacial age. We may, of course, dismiss the possibility that any species survived *all* the glacial ages in Britain, but the term "preglacial" is often used there to signify "antedating the earliest glaciation of which we have first-hand knowledge". Hence if for "preglacial", in the works of Praeger (1932; 1939) for example, we read "last interglacial" or, better, "Warthe-Brandenburg interval", the possibility becomes worthy of serious discussion.

One group of these facts can be disposed of rather easily. A small group of American species, most of which are confined to Ireland, include the ladies' tresses, *Spiranthes gemmipara* and *S. stricta*[2], the blue-eyed grass *Sisyrhynchium angustifolium*, the water plants *Eriocaulon septangulare* and *Naias flexilis*, and the fresh-water sponge *Heteromeyenia ryderi*. These are authentic American species, and only one is found east of Britain; but this one, *Naias flexilis*, though its scattered distribution in the Baltic states shows it to be a relict, is known on stratigraphic evidence to have been common in Europe in Boreal time (Sandegren, 1931/1932). Evidently this plant holds the key to the distribution of the others, and all are probably relicts of a former circumpolar distribution. The *Heteromeyenia* is particularly interesting, for the Irish records include an American subspecies as well as the typical form, while the only other record outside North America comes from the Faeroes (Arndt, 1926; 1928). There is another member of the genus, however, in Japan, a fact that considerably reduces the mystery. Some European writers ignore the fact that a small and equally interesting group of species indicates connections in the opposite direction: *Carex Hostiana*, for example (Marie-Victorin, 1938), and, curiously enough, the characteristically German fresh-water sponge *Trochospongilla horrida* is known from two localities in Illinois.

The remarkable thing about such distributions is not their disjunction, for many terrestrial species are found on both sides of the Atlantic Ocean, and not all of them are circumpolar; it is their asymmetry, *i.e.*, their unequal ranges on the two continents, that attract attention. But asymmetry of range means little by itself. The cases of *Tsuga canadensis* and *Dulichium spathaceum*, now extinct in Europe

[2] *Spiranthes Romanzoffiana*, cited in this connection by Marie-Victorin (1938) among others, does not occur in Ireland but was formerly confused with the two species that do (Praeger, 1928).

and the converse case of the horses[3], warn us that the histories of Pleistocene restriction or extinction in Europe and North America, though similar, have not been identical. The point is important, because asymmetric distributions have often been thought to result from a land bridge across the Atlantic. Proponents of such a bridge should explain why the only animal to cross from America to Ireland, out of all that might have done so, is a fresh-water sponge, which has gemmules resistant to drought and freezing. The American species in Ireland, then, are to be regarded as relicts of a former more extensive, perhaps circumboreal, distribution, and prove nothing about Pleistocene survival *in situ*.

The Lusitanian element in the biota presents a much more baffling problem. There is a group of plants, such as *Arbutus Unedo*, *Saxifraga umbrosa*, *Erica mediterranea*, and *Pinguicula grandiflora*, and of animals, such as the Kerry slug, *Geomalacus maculosus*, and a woodlouse, *Trichoniscus vividus*[4], which live in Ireland, most of them in the southwest corner, some of them also in southern England, and are then absent from some or all of the French coast, reappearing in Spain, Portugal, or even the Mediterranean coast. How did they get into Ireland? Though we may accept Praeger's contention that the seeds of the plants could not survive a journey through salt water, it is not unlikely that some of them have been distributed by migrating birds. Species such as the bug *Aepophilus bonnairei* (China, 1930), which live on beaches and could easily be rafted across a water barrier, should be excluded from this discussion. Yet there are some critical species, notably the Kerry slug, that seem absolutely to require a land bridge.

It is important to realize that the puzzle presented by these species rests wholly on their occurrence in Ireland. A Lusitanian pattern such as that of Figure 11E is obviously a special case of the pattern shown in Figure 11D and is most simply interpreted as a case of disjunction by restriction since the postglacial climatic optimum. Though such species have evidently followed a continuous coast line that is no longer continuous, the Boreal coast line will serve the purpose so far as England is concerned. A continuous Boreal coast line extending as far as Ireland, however, seems to be excluded by the geologic data, for all the evidence indicates that Ireland was isolated from England by the postglacial rise of sea level. In Boreal time England and Ireland, though considerably closer than they are today, must have been separated by the broad estuary of the "Irish Channel river" and by deep water in the Sound of Jura. Moreover, even though one argues that the floor of the Irish Sea has been modified by post-Boreal submarine erosion to such an extent that it is no longer possible to reconstruct its Boreal topography, early isolation of Ireland from England is clearly indicated by the mammal fauna, and the biogeographer is confronted with a dilemma of the most uncomfortable sort. If the species in question (a) are warmth-loving types that could not have entered Ireland in late-glacial time, (b) are found in Ireland, and (c) required a land bridge to get there, the conclusion seems inescapable that they must have survived glaciation somewhere in Ireland. But how can warmth-loving forms, particularly those which, to judge from their occurrence in southwestern Ireland, require *warm winters*, have lived through a glacial age within a few miles of an ice sheet?

The excruciating quality of this riddle should not be minimized, and only further research,

[3] It is instructive to invent a hypothetical but plausible distribution for the horses, and to try to imagine what conclusions would be reached from it if paleontologic knowledge were confined to the western European Pleistocene. The horse is now known, say, from eastern Europe to Mongolia, and as a Pleistocene fossil from western Europe; rather distinct relatives are in Africa, while a typical *Equus* still lives in southeastern United States (we know that horses lived in Florida during the Pleistocene, and lasted until postglacial time in the Southwest, so this is quite reasonable). Biogeographers might then say that the horses obviously arose in central Asia, still the center of distribution of the group, and reached eastern North America by way of a land bridge across the Atlantic. When asked why the migration could not have gone the other way, they would answer that there is no evidence that the horse now goes far enough north in Siberia to have used the Bering bridge, and in any case there ought to be some relicts in the western United States showing this route of dispersal.

[4] The woodlouse *Platyarthrus hofmanseggi*, which lives in ant nests, has been cited as a Lusitanian form (Charlesworth, 1930), though it does not appear in Praeger's list (1932). This species has recently been discovered in Connecticut (Brooks, 1942) and is evidently a peregrine form, like the common earthworm *Lumbricus terrestris*.

directed particularly to the geology of the Irish land bridge, can provide the answer. It may be in order, however, to point to a possible biogeographic weakness in the argument. If the geologists can prove that there was no continuous land connection to Ireland in Boreal time, as they probably can, then it must be remembered that points (a) and (c) above are based on biologic evidence alone, and they too must be subjected to searching inquiry. And it may well be found that point (c) is an illusion. The recent history of biogeographic science warns us that some of the most universally accepted land bridges have foundered almost overnight, and this Irish one may not be so strong as it looks. We really know little about the biology of the Kerry slug, and, if it can be shown that it and a few of its fellows succeeded in crossing the Boreal Irish Channel, while such forms as the mole, the shrew, and the voles did not, the whole case for survival in Ireland during the New Drift glaciation will fall apart.

The Lepidoptera.—The butterflies of Great Britain have recently been treated elegantly and comprehensively in a nontechnical book by Ford (1945). Butterflies, of course, are not particularly favorable for zoogeographic studies, since they all can fly, and some of them (which however are excluded from Ford's discussion) are migratory. They have the compensating advantage of being extremely well known, systematically and geographically, and the British list is eminently manageable (68 species). The discussion of the British problem can therefore profitably be concluded with an account of Ford's conclusions, taken together with those of Beirne (1943).

Ford divides the nonmigratory butterflies of Britain into four groups, plus a group of two unanalyzable species:

Group I. Of the three alpine or northern species, which evidently reached the British Isles during glacial retreat, two, *Erebia epiphron* and *Coenonympha tullia*, are believed to have arrived after an earlier glacial age than the third, *Erebia aethiops*. The third is considered to have immigrated after the last glaciation and is placed in Group III. The evidence for the distinction is that the first two have crossed to Ireland, one also having reached the Shetlands, and that both are subspecifically distinct from Continental forms. As a land connecti with Ireland probably did not exist after t climax of the last glaciation, the first two m have arrived earlier than the third, which not found in Ireland and is not subspecifica distinct. If we could be sure (a) that the speci of Group I absolutely require a land brid and could not do even a little island-hoppi and (b) that there has been no land connecti with Ireland serviceable for butterflies sin an earlier glacial age than the last, this hypoth esis would be more convincing than it is. Sp cies that are surely postglacial immigrants England and whose populations are augmente occasionally from across the Channel are o course not likely to show subspecific distinctio but isolation in Ireland is sufficient to permi taxonomic differentiation without any gre antiquity being implied.

Group II. Here are placed the butterfli supposed to have arrived during the last inte glacial age (though it would presumably b proper to consider them as immigrants duri the Warthe-Brandenburg interval). The ev dence for antiquity is of different sorts. O division is found in Ireland, and those that a isolated in the south of Ireland are supposed t have been pushed there by the last (read "Ne Drift"?) glaciation, while others have spre over the rest of Ireland once more. Anoth division is not found in Ireland, but is repre sented by different subspecies in England a Scotland; the brown argus, *Aricia agestis*, sho a zone of hybridization where two subspeci have come into contact along the Scotti Border, so that it would appear that the Sco tish subspecies survived glaciation somewhe in Scotland. Still others, having distinct sub species either in Ireland (the Irish *Pieris no* being exceptionally well differentiated) or i small localities in England (such as the lar copper, *Lycaena dispar*, and the swallowtai *Papilio machaon*, in the Fenlands), seem fro their isolation to be relicts of a wave of migr tion antedating postglacial time. Others, su as the green hairstreak, *Callophrys rubi*, an the small blue, *Cupido minimus*, cannot be co ceived of as migrants across a water barri yet they have reached Ireland. This evidence not all of equal weight, and the greatest impo tance is attached to taxonomic differentiati

a treacherous criterion in an insular fauna. It is also remarkable that two of the handsomest and most distinct British subspecies (one of which, the large copper, is extinct, but has been artificially replaced by the Frisian Islands form) occur in the Fenlands, an environment that was certainly very different from today as recently as Roman time (Godwin and Clifford, 1938; Godwin, 1940). Elsewhere in Ford's book one learns of some startling expansions and contractions of range within the period of scientific collecting of British butterflies, so it would appear that isolation in a small and unusual locality is not reliable as a testament of age.

Group III contains the Scotch argus, *Erebia aethiops*, already discussed under Group I.

Group IV contains the species certainly to be regarded as postglacial immigrants, some of which have spread to Scotland, but the majority of which are confined to southern England. No British butterfly falls in the Lusitanian pattern, while the occurrence of one American species, the monarch, *Danaus plexippus*, is amusing, for this wide-ranging, extensively migratory insect is undoubtedly introduced into Britain from across the Atlantic with appreciable frequency.

These remarks should have conveyed the writer's belief that this analysis of Ford's, though exceptionally well thought out, falls short of the proof required before Pleistocene survival in the British Isles can be accepted. There are, as he admits (p. 321) "extensive sources of error", of which the principal one is the temptation to rely unduly on taxonomic differentiation. It follows that the comparison between the "Pleistocene arrivals" and the "Holocene species" (Ford, 1945, p. 321) in which it is shown that 45.5 per cent of the former but only 10.5 per cent of the latter have formed subspecies, and that the difference is statistically significant, comes within about 90° of being a circular argument.

Beirne's analysis (1943), though more synthetic than Ford's, is equally interesting. It is based on the whole lepidopteran fauna, 792 native British species. They can be divided into two groups both in Great Britain and Ireland: Groups A and C are confined to certain limited areas or have discontinuous ranges, and many of them have formed local races or subspecies; Groups B and D contain wide-ranging species, and few of them show any taxonomic differentiation. The two faunas are therefore thought to be of different age in Britain, and it is concluded that the first was introduced during disappearance of the last ice sheet and that the second is postglacial. It is then argued (and here the validity of the last conclusion is assumed without further question) that one can infer (a) from the regions where the A and C species are now mainly found, and (b) from the food plants of these species, what climatic conditions are likely to have prevailed at the time of the "late-glacial" introduction; these climatic conditions are inferred to have been somewhat more severe than today, especially in the mountains. Proceeding from the premise of the first conclusion, that the two waves of migration were separated by a considerable period of time, during which a climatic deterioration took place, Beirne considers the Allerød oscillation (Zone II of Jessen and Farrington) as the most likely time of introduction of the first wave, while the dissection of ranges took place in the following Zone III (Upper Dryas). No British Lepidoptera show a Lusitanian pattern, but six endemic moths in Ireland are local representatives of Iberian species; as all fall in the "late-glacial" group, the true Lusitanian forms must have been introduced earlier; "it is therefore not improbable that they date from the last interglacial" (p. 49). This last is a curious inversion of the usual line of reasoning, which would state that the true Lusitanian forms, not being taxonomically distinct in Britain, must have arrived *later* than the species that have given rise to endemics.

The crux of the whole argument, of course, is the assumption that, because two groups can be distinguished on the basis of taxonomic differentiation and geographic isolation, two waves of immigration are represented. The writer believes this is not necessarily the case. All species cannot be distributed equally widely, even when all are introduced at the same time. The isolated, local distributions, with numerous disjunctions of range, on which Beirne relies for his assignment of species to Groups A and C, though they imply a change of climate in many cases, do not always imply glaciation, or

even cooling. It seems most improbable that so large and heterogeneous an assemblage of species could date from the Allerød oscillation, for some of these Lepidoptera are associated as larvae with forest trees (oak, alder, birch, and even elm), and there is abundant evidence that true forests were absent from the British Isles until later (Zones IV and V). Many of Beirne's cases, then, are probably relicts of the postglacial climatic optimum, now restricted to especially favorable districts. Again, as Ernst Mayr has pointed out (oral communication) not all disjunctions of range are due to restriction; some are due to expansion, and it is easy to underestimate the ability of a species to disperse over unsuitable territory.

In summary, the fauna and flora of the British Isles have certainly (in the majority of cases) or probably (in most of the rest) immigrated since the retreat of the latest ice sheets. Because England was firmly joined to Europe until after the Boreal phase, when forests covered northern Europe, Great Britain is a truly continental island in respect to its biota, though there are many interesting lacunae and many interesting endemic forms[5]. Ireland, with its more marked impoverishment, presents a special problem. There is no evidence of a land connection with England since well before Boreal time, but most of the biota could have (and evidently did) immigrate over chains of islands, this process being somewhat easier during the Boreal phase than it is now. The occurrence of some extremely interesting relicts, including the "American element" and especially the Lusitanian forms, has repeatedly been explained as the result of survival through at least one glacial age. Although this does not seem at all likely, it cannot yet be absolutely ruled out.

Some Minor Land Bridges

The discussion of the British Isles, and especially of the Isle of Man, shows that the data of biogeography have a very important bearing on Pleistocene changes of sea level. To the geologist, in fact, it may seem that this is their only sphere of service, biogeographic inferences as to glacial refuges being highly speculative and easily refuted by healthy stratigraphy. In subsequent sections changes of level will receive attention in connection with South Africa and with southeastern Asia. Much more could be said about such changes in northern Europe, but an exhaustive review of the biota of islands peripheral to the Continent, though it would be well worth while, must be deferred for a future report, and should probably be undertaken by someone with a knowledge of the Scandinavian languages. Remarks in this section will be confined to some of the more familiar and accessible problems.

The first of these is the island of Bornholm, in the Baltic between Germany and Sweden. Its recolonization by animals and plants is certainly of postglacial date. Moreover, postglacial land connection with the mainland is definitely indicated, for example, by the reptiles and amphibians, for the fauna contains three lizards, two snakes, eight frogs and toads, and two newts, plus the tortoise *Emys orbicularis*, known as a postglacial fossil (Hecht, 1933). Detailed knowledge of the history of the Baltic, summarized in many familiar sources, indicates that Bornholm was joined to Germany at the time of the Ancylus Lake. The exact position of the Ancylus shore line in this region is difficult to fix, as it is now under water, but the occurrence of stumps containing peat of Boreal-Atlantic age has been reported in depths as great as 37 meters (Isberg, 1927; Pratje, 1934). The shore line is therefore taken as approximately coextensive with the 40-meter isobath[6], and on this assumption Bornholm was part of a peninsula. Nothing about the fauna is inconsistent with the view that it arrived in Boreal time, but Hecht's suggestion that it arrived from eastern Europe *via* Pomerania rather than along the route taken in the postglacial colonization of Denmark and Sweden is without foundation. Hecht maintained that the Bornholm representative of the water snake *Natrix natrix* was

[5] On the estimate of Heim de Balsac (1930), of the 43 British land mammals, excluding bats, rats, and doubtful species, 12 are endemic, while all the rest are subspecifically distinct. The taxonomic lines have certainly been drawn too finely in this case.

[6] An emergence of 80 meters during Ancylus time, which would join even Gotland to the German coast, and which is assumed by Lindroth (1933) to account for the occurrence there of the weevil *Tropiphorus obtusus*, is entirely unlikely.

the eastern European subspecies *scutata*, but Pfaff (1935) showed that this identification rested on three specimens, and that there is no difference between the Bornholm form and the subspecies *natrix* of Denmark and Scania.

The colonization of islands on continental shelves has important implications for the strictly biologic study of speciation and evolution, as well as for Pleistocene geography. One of the most famous cases, that of the lizards (*Lacerta sicula*) of the small islands off the Istrian coast, should not be left entirely out of account, even though its geologic basis is unsatisfactory. According to Kramer and Mertens (1938) there is a quantitative relationship between the degree of taxonomic differentiation among these lizards and the *age* of the islands on which they occur. The *area* of the island is a complicating factor, owing to the rapidity of evolutionary change in small populations (the Sewell Wright effect), but as Huxley (1943) puts it, there is supposed to be a definite "partial correlation" with age when area is held constant, and with area when age is held constant. Mayr (1942) points to a third factor—*distance* from the mainland. It must occasionally happen that a lizard is rafted across the relatively short distance; the chance of this is of course greater for the nearer islands. Reference to the original work shows that the statistical treatment is inadequate. The concept of partial correlation, which has a definite statistical meaning and could appropriately have been applied here, does not appear, but instead Kramer and Mertens take the algebraic sum of the depth of the channel plus the area, the latter being added in as though it had a negative sign. The sum is then compared with the degree of taxonomic distinctness of the lizard population, expressed in arbitrary units from 0 to 4. This quantitative technique might be acceptable, crude as it is, but the geologist must ask on what grounds the depth of water between the island and the mainland is regarded as a function of age. The underlying assumption, of course, is that the sea rose *at a uniform rate* from its low stand during the last glacial age. This level is taken as −90 to −100 meters, following Dubois; the greatest depth inside the islands is a little more than 30 meters; therefore the islands were formed in the last half of postglacial time, the ones with deeper channels being older. But nothing we know about eustatic rises of sea level justifies the assumption of a uniform rate of rise throughout postglacial time. If assumptions have to be made, it is much more reasonable to assume that the rise was hyperbolic, as we know it was in the British Isles. But on this assumption most of the rise had been completed during the first half of postglacial time, and all the islands are of approximately the same age. The differences in the lizard populations, which are undoubted, are therefore presumably related to area and to degree of isolation, as well as to other factors not so readily ascertained, but more data are needed for a quantitative evaluation of the relationships.

This example from the Mediterranean region brings us to the problem of Corsica. A volume of the *Mémoires de la Société de Biogéographie* (Tome 1, 1926) is devoted to this island, but it is in some ways the least satisfactory of the series, owing to the almost complete failure of its authors to consider the colonization of Corsica as a Pleistocene problem. A gecko (*Phyllodactylus europaeus*) occurs there, for example, as it does on several other Mediterranean islands, and, as this is the only Palaearctic gecko, Joleaud finds it necessary to go back to the Permian to account for its distribution. But if we discount such wildly improbable hypotheses, and ignore the large amount of discussion of the ancient land mass "Tyrrhenia", which is supposed to have foundered in the eastern Mediterranean, Corsica and Sardinia raise several interesting questions for the Pleistocene biogeographer.

As would be expected from its size and its isolation, there are some distinct varieties of mammal on Corsica, some of them perhaps meriting specific status. The white-toothed shrew *Crocidura russula* is represented on Corsica by *C. cyrnensis*, and on Sardinia by *C. ichnusae;* rather different shrews of this genus are found on each of several other Mediterranean islands, and a comparable group of insular species also characterized the extinct shrew genus *Nesiotites* during the Pleistocene (Bate, 1944). The weasel *Mustela boccamela boccamela* is endemic to Sardinia, and a distinct race, *M. b. corsicana*, occurs on Corsica. The red deer

Cervus elaphus corsicanus is not especially close to *elaphus*, according to Bate (1943), though the various Mediterranean deer are poorly known; the Corsican form is also known as a Pleistocene fossil. Distinct subspecies of hare, *Lepus europaeus*, are also said to occur on the two islands, *L. e. corsicanus* being the Corsican form. Apart from these, however, there is scarcely any endemism, and though the fauna of Corsica includes the hedgehog, the fox, the badger, the lynx, several rodents, the wild boar, and the sheep, not to mention several bats, none is more than subspecifically distinct from its mainland representative. Subspecies identical with the Italian form are: *Erinaceus europaeus italicus*, *Vulpes vulpes crucigera* (possibly introduced), and *Apodemus sylvaticus dichrurus* on Corsica, *Martes martes latinorum* and *Felis ocreata sarda* on Sardinia. Evidently the isolation of Corsica from Italy is not of very long standing. Moreover, the list of mammals contains species, any one of which might have crossed a water barrier, but which taken collectively form a balanced land fauna and therefore imply land connections in the recent past. The mammalian evidence is confirmed by the occurrence of the fresh-water flatworm *Planaria alpina* on Corsica.

Could these species have entered Corsica during the last glacial age, when sea level was lower? At first sight it seems improbable, for the strait that separates Corsica from Italy is between 180 and 360 meters deep. The evidence from near-by Versilia (Blanc, 1937) shows that during the last glacial age the sea was at least 100 meters lower than today. There is nothing to prove that it could not have been lower, but, as this figure agrees so well with estimates of the eustatic lowering of sea level in other parts of the world, it is not safe to go beyond it at present. The deep channel, however, is very narrow: less than 6 miles of open water would separate Corsica from the shelf north of Elba if the sea were lowered by 180 meters, and the distance would probably not be much greater if the 100-meter isobath were taken as a guide. This compares with a present gap of 50 miles, and submarine deepening of the channel could easily have occurred here since the sea level began to rise.

The implication of the low degree of endemism in the mammal fauna is so definite that it seems that this must be what happened. It should be noticed that the most distinct forms on Corsica are also represented by distinct forms on Sardinia, though the two islands are virtually one; no one would suppose that they have been separated from each other by water since the last glacial age, yet their isolation has been sufficient to permit speciation. Nothing could show more clearly that all animals do not form species at the same rates, and this argument therefore eliminates the Corsican endemics as evidence of a longer isolation.

One of the lacunae in the Corso-Sardinian fauna also can be used to support the dating of the invasion of Corsica. There are no moles today on either island, though Sardinia had one in (probably Lower) Pleistocene time (Bate, 1945). This, however, was *Talpa tyrrhenica*, a member of the *T. romana* species group, and not allied to the typical moles of temperate Europe. The absence of a modern mole points, as Bate says, to adverse climatic conditions, followed by isolation. Evidently the animals that were able to use the land bridge to Corsica were species that took refuge in Italy during a glaciation, and this conclusion is supported by the occurrence of several of them (*Crocidura russula*, the badger, the lynx, the wood mouse, the boar, and the deer) in the Mousterian rock shelter at Gibraltar (Bate, 1928), where they were associated with the alpine chough and the great auk.

One remarkable Corsican species should also be recorded. The ochotonid rodent (cony) *Prolagus sardus* occurred throughout the Pleistocene both in Corsica and Sardinia and appears to have survived until the seventeenth century on the small island of Tavolara off Sardinia (Tobien, 1935). The genus is now extinct, and this animal seems to have been an extraordinarily late survival of the Lower Pleistocene mammal fauna of the Mediterranean region. Subspecific differentiation between Corsican and Sardinian populations can be demonstrated in the fossil material. Associates of *Prolagus* in some deposits include four other extinct genera (*Nesiotites*, *Enhydrictis*, *Tyrrhenicola*, and *Rhagamys*), whose occurrence is the basis for the dating of these deposits as Lower Pleistocene. The survival of one archaic element, however,

does not prove that the whole fauna is of any great antiquity. Other species that must have reached the islands via earlier land bridges include *Elephas antiquus lamarmorae*, known from Sardinia. This is a member of the species group that includes the Maltese elephants (Vaufrey, 1929), but the land bridge to Malta is well established (Trechmann, 1938) and does not require special pleading.

Conclusions

This chapter, as has been pointed out by several members of the Committee on Interrelations of Pleistocene Research, needs a summary, in which the general reader, a geologist unconcerned with the taxonomic and evolutionary aspects of the biologic data, can quickly survey the biologist's conclusions. The following chapter, on North America, deals with some of the same biogeographic problems as this one, plus some that have been omitted from this chapter owing to the writer's unfamiliarity with the European literature. One of the final sections of the next chapter, in which account is taken of pluvial as well as glacial climates of the Pleistocene, makes an easy transition to the chapters on Africa and Eastern Asia. It seems best, therefore, to defer the summary of European biogeography until the two northern continents can be appraised together.

Pleistocene Biogeography of North America

Outline

North American biogeography appears to the writer to be far more difficult to summarize than European, and this is at first sight surprising in view of the vastly greater quantity of the European literature. North America is much larger, however, and has fewer students of the Pleistocene than Europe. Although in some respects, such as the glacial stratigraphy of the Middle West, North America is about as well known as Europe, there are certain extremely serious gaps in our knowledge. Not only are existing ranges of species very inadequately known, so that discussion of Pleistocene influence on recent distribution is hampered by data at once too voluminous and too sketchy, but it also happens that our knowledge of interglacial deposits is extremely meager. The wealth of information on Pleistocene climatic and other environmental conditions and on past ranges of species available to European workers is almost missing in orth America. This inadequacy, part of the larger difficulty that there is no real Pleistocene stratigraphy except in a local sense, is the greatest existing obstacle to progress in Pleistocene research, and it should be the task of this Committee to alleviate it.

The program of attack in this chapter is roughly the same as in the last: after a summary treatment of the Pleistocene stratigraphy, abstracted almost entirely from Flint (1947), and a somewhat more detailed consideration of the postglacial stratigraphy of the eastern United States, existing ranges and their problems are discussed. Certain curious disjunctions of distribution are brought forward, and it is shown that most or all of them are explicable in the light of postglacial climatic changes, though due weight will be given to the opinion of many that certain species have survived one or more glacial ages in centers of refuge in boreal America. No biogeographic problem so full of interest for students of diverse disciplines and so productive of *ad hoc* research as the biogeography of the British Isles has yet emerged in North America; but the tracing out of Pleistocene stream connections by means of fish and mollusk distributions raises questions of almost equal interest, and the chapter concludes with an account of our fragmentary knowledge of this subject.

Pleistocene Stratigraphy

The writer is unable to add any significant new data to the summary of the state of knowledge given by Flint (1947). Accordingly the main outlines of the stratigraphic column are reproduced in Table 6 for ready reference.

Information on North American interglacial fossil floras, especially on fossil pollen, is astonishingly deficient. It would seem that geologists generally do not appreciate the possibility of microstratigraphic refinement when interglacial deposits are studied. Great quantities of vertebrate and molluscan fossils, and some wood,

have been collected, but the naming of this material has often been entrusted to inexperienced hands, and too often reports have been written by workers whose geographic horizon incidentally to other sorts of areal surveys, and chiefly by stratigraphers of an older school. To them it seems reasonable to expect the fossil species of one horizon to be largely extinct, to

TABLE 6.—PLEISTOCENE STRATIGRAPHY OF EASTERN NORTH AMERICA, WITH PRESUMED EUROPEAN EQUIVALENTS

Glacial ages and subages capitalized, interglacial ages and subages italicized. After Flint (1947)

North America		Northern Europe		Alps
WISCONSIN	MANKATO *Two Creeks* CARY *Interval* TAZEWELL *Interval* IOWAN	WEICHSEL	BRANDENBURG *Interval* WARTHE	WÜRM
Sangamon		*"E" Interglacial*		
ILLINOIAN		SAALE		RISS
Yarmouth		*"D" Interglacial*		
KANSAN		ELSTER		MINDEL
Aftonian		*"C" Interglacial*		
NEBRASKAN		DONAU		GÜNZ

is limited by the boundaries of the State in which they live. Such workers are likely not to realize that the existence of a fossil species today somewhere within the confines of their State is no warrant for the assumption that the climatic conditions surrounding the organism were essentially like those of today; the existing representatives of the species may be extremely rare, local, or relict. Again, even when the stratigraphic position of the interglacial deposit can be stated, the level of the fossil within the deposit itself is often not regarded as worth recording. The preservation of an interglacial peat or soil deposit under the drift of a later ice sheet is highly improbable, and sections recording the complete history of an interglacial age must be very rare. As most of the known sections are incomplete, microstratigraphic methods would seem almost imperative for correlation, yet they are almost never used. The fundamental barrier seems to be that Pleistocene geology is studied in North America be related faunistically and floristically to species of equivalent age, and to be taxonomically distinct from fossils of earlier and later ages. Within the Pleistocene this is simply not true: in the absence of any great degree of evolutionary change and extinction, it is only by detailed knowledge of geographic distribution of species, present and past, and by attention to ecologic associations, that the biology of fossils can yield results of geologic importance.

The advantages of close study of existing ranges of fossil species are well illustrated by the recent work of Steere (1942) on the mosses of the type deposits of the Aftonian Interglacial stage of Iowa. Thirty-three species have been found in these deposits, some of them in a remarkable state of preservation. While four of these are extinct, no great difference from modern floras is implied by the fact, for all four belong to plastic genera, and one may be a member of the genus *Neocalliergon* Williams, described as new from the late-glacial deposits in

Minneapolis (Cooper and Foot, 1932). (Williams' species, *N. integrifolium*, is now known from the Peorian interval in Minnesota, according to Rosendahl, 1948). Consideration of the present geographic ranges of the remainder indicates that "the Aftonian interglacial . . . was much colder and wetter than at present, with a climate like that now existing five hundred to a thousand miles farther north" (Steere, 1942, p. 100). But Steere does not discuss the possibility that these deposits do not record the whole of the Aftonian, and the pollen data of Lane (1941), particularly those for the Dennison beds (also in Iowa, but farther north), imply that at the climax of the interglacial conditions in Iowa were about as warm and as dry as at present, as shown by a maximum of deciduous tree and herbaceous pollen. Lane's pollen data for the Union County deposits, from which Steere's mosses came, are unsatisfactory owing to the small number of grains obtainable by the KOH method, but they do suggest that some attention to the microstratigraphy of the fossil mosses might have been profitable. For this omission Steere is not responsible, since he did not make the collection.

Steere argues that mosses deserve more attention from Pleistocene geologists than they have received, for there are likely to be more species in a given deposit and their ecologic requirements are more narrowly drawn than in the case of phanerogams. It may be doubted, however, that mosses have been deliberately slighted by geologists. What has been neglected is the kind of close attention to detail in the field that distinguishes European from American stratigraphic work (at least where *interglacial* deposits are concerned), the technical refinement that might have made Steere's excellent studies more illuminating than they actually are.

The recent paper of Rosendahl (1948) on the Pleistocene flora of Minnesota deserves mention here. In this account 126 species are listed, 76 of them from a single well boring dated as Peorian. There is an extraordinary preponderance of white spruce, *Picea glauca*. In this otherwise admirable work there is again no recognition that a "deposit" may have any internal stratigraphy.

It seems, then, that while long lists of Pleistocene fossils have been assembled from North America, as by Hay (1923; 1924) and Baker (1920), we really know extremely little about biogeographic conditions during the epoch as a whole. Flint's account condenses all the essential information into a few short paragraphs and shows that what we know is just about what one would predict if he knew about multiple glaciation but had no other information. That is, during the glacial ages the fauna and flora were pushed south by the ice sheets, while during interglacial ages the biota expanded, a given species going as far north as it does today or in some cases a little farther. The interglacial climates varied from cool to about as warm as today and back to cool again as the next ice sheet approached, but the fossil evidence on which this almost banal deduction is based is deplorably scanty. On the finer points of the migrations of plants and animals, on the location of refuges, on the mechanics of speciation by glacial isolation and subsequent overlapping of ranges, and on many other vital details American biogeography is nearly 50 years behind the European. The next section will show that insofar as postglacial time is concerned a similar lag is evident, though it may be estimated at 15 rather than 50 years.

Postglacial Stratigraphy

Pollen analysis.—In postglacial pollen analysis American workers, though somewhat slow to employ the technique, have been making great strides, and the situation, in the eastern United States, at least, is nearly ripe for an informative summary. Several have been attempted from time to time (Sears, 1935a; 1935b; 1938; 1948; Cooper, 1942c; Fuller, 1935; Cain, 1939; 1945; Eiseley, 1939), and a new interpretation follows. Its essential outlines are given in Table 7.

For many years, apart from macroscopic fossils in late-glacial deposits (Hollick, 1931), we have had no evidence of a tundra vegetation preceding the episode of spruce-fir forests with which the American pollen diagrams open. It has often been pointed out that borings in peat bogs are not likely to reach sediments deposited in the vicinity of active ice, since most peat bogs occupy kettles, kettles imply dead ice masses, and small masses of dead ice probably

TABLE 7.—POSTGLACIAL POLLEN CHRONOLOGY FOR EASTERN NORTH AMERICA

Zones	Climatic Interpretation	Wisconsin and Minnesota	Illinois and Indiana	Ohio	New York	Northern New Jersey	Connecticut	Maine and New Hampshire	Nova Scotia
C3	Cooler, Moister	Return of Spruce at some localities	Oak-Hickory; Elm Declining	Oak-Beech	Oak-Hemlock	Oak-Chestnut-Pine	Oak-Chestnut	Hemlock; Spruce Rising	Spruce Rising
C2	Warm, Dry	Pine Declining		Oak-Hickory	Oak Maximum	Oak-Hickory-Chestnut Beech Minimum	Beech III Oak-Hickory	Oak Maximum	Oak Maximum
C1	Warm,	Pine-Oak-Elm	Oak-Elm	Oak-Beech [Hemlock]	Oak-Hemlock	Beech II Oak-Hemlock Beech I	Oak-Hemlock	Hemlock-Oak	Hemlock-Oak
B	Warmer, Dry	Pine	Pine	Pine	?	Pine	Pine	Pine	Pine
A	Cool	Spruce-Fir	Spruce-Fir	Spruce-Fir	Spruce-Fir	Spruce-Fir	Spruce-Fir	Spruce-Fir	Spruce-Fir
	Deglaciation	Tundra Flora (known pollen-analytically in Maine only)							

melted out some time after the first wave of plant colonists had swept on beyond the site of the borings. Moreover, sediments older than the peat or lake mud with which the record of organic deposition begins in our small lakes and bogs are in general poor in pollen, troublesome to analyze, and have not even been collected by many American workers. Thus if there is a record of tundra vegetation immediately following on the heels of the retreating ice sheets, geologic circumstances and the mental habits of pollen workers may have conspired to make them miss it. The writer still believes that this is the correct explanation for the lack in North American pollen diagrams of a phase corresponding to the Late-Glacial in Europe. Some workers, however, have come to doubt that there ever was a belt of tundra vegetation peripheral to the retreating ice, at least as far south as the United States. The evidence in favor of this view is largely negative, though considerations based on fish distribution, presented in a later section, strongly suggest that the tundra zone was very narrow in the Middle West. An argument based on data from Minneapolis (Cooper and Foot, 1932), showing that an upland forest grew within 250 miles of the late Mankato ice sheet, seems irrelevant, for 250 miles leaves plenty of room for tundra. However, it is the general position of Braun (1947), as discussed below, that *beyond* the Pleistocene drift border there was very little effect of glaciation on the vegetation.

At any rate, evidence of a tundra phase has at last come to light in pollen data from Maine (Potzger and Friesner, 1948). The data are entirely inadequate for a thorough study of the problem, for in their analysis of the thick layer of rock flour underlying the peat in the Maine bogs Potzger and Friesner failed to use special methods for concentrating the pollen, and made only a few counts of 10 or 20 grains each. In several of the deep samples, however, the non-tree pollen, especially of grasses and composites, reaches values from 25 to 50 per cent of total forest tree pollen, and in one sample the percentage of grasses alone is 122. Such figures provide a strong indication of a treeless or very sparsely wooded country, and closer analysis of samples like these seems almost certain to bring forward the first North American account of the "Late-Glacial" that can be connected pollen-analytically with the "Postglacial" as Firbas and others have done.

The strictly postglacial pollen diagrams from Connecticut (Deevey, 1939; 1943) and Massachusetts (Deevey, 1948b) have been divided into five "zones" (horizons), following the practice of European workers. As these correspond closely with the five zones recognized by Sears (1932) in Ohio (but with designations subsequently changed; Sears, 1942a), the position adopted here is that the whole eastern United States can be fitted into this sequence. There are certain difficulties for this interpretation, particularly in some of the diagrams from the middle West. But the pattern is so clear over so wide an area that it would seem that variations must reflect local aberrations of the vegetation rather than departures from the climatic sequence implied by the "normal" diagrams.

There is little question of the validity of the spruce-fir zone, *A*. When a diagram anywhere north of the drift border in eastern Canada and the eastern United States fails to show it, this failure is now regarded as proof that the boring is incomplete. Within the interval, however, there are variations from place to place. Most interesting of these are oscillations of the spruce curve (rise to a maximum before the end of the phase). One such oscillation in southern Connecticut has been equated to a local readvance of the ice border, of which there is independent evidence. In Indiana, and especially in Wisconsin and Illinois, one has the impression that bogs near but outside the limits of a later Wisconsin substage usually show a spruce oscillation, while those farther from the ice or on the latest Mankato drift do not. (*See* data cited by Deevey, 1939.) A general summary of this kind of detailed stratigraphy must await a better knowledge of the late Wisconsin substages outside the Lake States; and indeed, so far as the geologist is concerned, there usually are better ways of establishing a readvance of the ice than by looking for a spruce maximum in near-by bogs. The supposed relation between advancing ice and resurgent spruce forests, and the lack of such a relationship in some localities, is

merely one aspect of the relativity of pollen zones as chronologic horizons.

The next zone, *B*, is characterized everywhere[7] by a strong maximum of pine pollen. The resemblance to the European Boreal is too close to be ignored. Evidently in this interval the climate became considerably warmer and drier, and pines, presumably of different species (*e.g.*, *Pinus rigida* in New England, *P. banksiana* and *P. resinosa* in the middle West), found suitable habitats on the poorer soils. It is not implied that pine forests prevailed everywhere during this phase. The universal occurrence of large quantities of pine pollen (normally over 50 per cent) must mean that pines occupied at least the poorer soils while deciduous trees were still absent from the richer sites.

In the deciduous zones, *C*, regional variation within the eastern United States begins to emerge. This variation is responsible for the difficulties of correlation. Until an absolute chronology is available (and there is reason to believe that the new radiocarbon technique (Libby, Anderson, and Arnold, 1949; Merrill, 1948) will ultimately provide such a chronology) pollen sequences will ordinarily give only relative dating; even so, the predominance of hemlock in New England, of oaks and hickories in the middle West, and other regional differences in forest composition stand in the way of the simple interpretation on which correlation must be based. In the light of the clear and well-established sequence in southern New England, however, it seems obvious that the threefold division: oak-hemlock, oak-hickory, and oak-chestnut, has its ecologic and climatic counterpart in the succession: oak-beech, oak-hickory, oak-beech in Ohio, the beech representing relatively mesophytic, moist conditions (as compared with the hickory) in a region where hemlock is not abundant. In diagrams from northern New England and Nova Scotia, where oaks are relatively scarce, there is a maximum of oak pollen in the middle (*C2*), and the subsequent return of spruce and hemlock is therefore taken to represent *C3*. Proceeding in this way, as has been done largely by Sears and the writer in various publications, the chief difficulties are met in Illinois, Michigan, Wisconsin, and Minnesota, where a threefold division is often impossible to distinguish. Many Indiana diagrams[8] also fail to show a consistent subdivision of the *C* zones. But in some of those characterized by a steady oak curve there is a well-defined maximum of elm pollen above the pine zone, and this is here equated to *C1*. In Wisconsin and Minnesota, where large quantities of pine pollen often confuse the picture, there is nevertheless a steady decline of pine and a rise of oak or spruce either throughout *C* or throughout the part of the diagram that lies above the elm peak.

Table 7 accordingly embodies an interpretation of post-Boreal time that is reasonably certain for the whole region from Ohio eastward and that is extended westward with confidence that future work will support the correlation. However, it is possible now to go further, to refine the threefold subdivision of the *C* zones[9] in the eastern States. For this purpose reliance is placed on small but remarkably consistent fluctuations of the beech curve that were first noticed in Connecticut (Deevey, 1943) and northern New Jersey (Potzger and Otto, 1943). Two rises of beech pollen, across the *C1-C2* transition and across the *C2-C3* transition, are separated by a minimum at the time of the hickory maximum in practically all "normal" profiles from Maine to Ohio. ("Normal" profiles are those that show sufficient detail above the pine maximum, are not obviously truncated, and have not been seriously influenced by pines, spruces, etc., near the site of the boring.) At first sight the New Jersey diagrams seem to fit this picture extremely well. Closer study, however, suggests that the New Jersey profiles are truncated at the top, and that the second beech maximum in New Jersey corresponds to the first in Connecticut and

[7] A question mark is placed in the New York column of Table 7 because the only New York pollen diagram available (McCulloch, 1939) happens not to show a pine zone. It has occasionally been missed elsewhere.

[8] It is true, as Sears (1948) remarks, that many of Voss's (bog) profiles and others that have long seemed to resist the classification into three *C* zones are obviously truncated. This happy explanation cannot apply to profiles from Indiana and Michigan lakes, however (*e.g.*, Potzger and Wilson, 1941; Wilson and Potzger, 1943).

[9] This interpretation has not previously appeared in print, though it has been hinted at (Deevey, 1943; 1948b). It was presented orally at the New Jersey meeting of the Ecological Society of America in June 1948.

Ohio. But if this is so, the first beech maximum in New Jersey (for example in the Squires Corner bog) is so far unrepresented elsewhere.

A perfectly plausible phytogeographic explanation is at hand for the facts as they now appear and is indicated in Table 8. Beech, moving out from its center of refuge in the northern Appalachians, appeared in strength during *C1* in New Jersey, which was nearest the refuge; as it moved into Ohio, in the direction of a more continental climate, it became relatively dominant, and high percentages of beech pollen characterize *C1*. It also moved into New England, where it had been preceded by hemlock, as it had in Ohio as well. (*See* especially Ohio diagrams by Potter, 1947.) As climatic conditions during *C1* were more suitable for hemlock in New England, beech did not obtain a foothold there until the drier conditions of *C2* were approaching. On the other hand hemlock did not establish itself firmly in Ohio, and was quickly replaced by beech. But during *C2* conditions were drier everywhere, and hickory, moving eastward from centers of refuge in the middle West, brought about an interruption in the migration of beech and hemlock, which, though temporary in the long view, was nevertheless of fairly long duration. Renewed migration of beech took place during late *C2* and early *C3* and was perhaps followed by some retrogression in New England as the climate deteriorated and became suitable once more for hemlock and even for spruce and fir.

This explanation admittedly rests on slender evidence, for it requires three beech maxima in all, whereas no profile yet available shows more than two. Two of them, however, here regarded as II and III, are so well shown in most profiles and so difficult to account for on purely climatic grounds, that probably some other phytogeographic interpretation will have to be substituted if this one proves untenable. At the meeting where this hypothesis was put forward the writer was startled and gratified to learn from W. H. Camp that modern (and still unpublished) taxonomic studies have shown that there are three species of beech in eastern North America, instead of one, and that one of them (presumably that whose migration is recorded as Beech I in New Jersey) is an associate of the spruce-fir forest community in southeastern Canada.

The relativity of pollen zones as chronologic markers has been alluded to several times. We do not know that climatic zones moved regularly and gradually from south to north with the ice sheets, succeeding each other in space as they did in time. Pollen analyses show a transition from pollen of spruce and fir through pine pollen to pollen of broadleaf deciduous trees, the same sequence being repeated everywhere that profiles are available. This sequence certainly reflects phytogeographic movements, but it is only an inference that migrations of climatic belts were also involved. It seems a reasonable inference, and there are no present grounds for doubting it. But the time required even for the major plant migrations to be completed imposes an elasticity on the pollen chronology that may be serious if chronologic comparisons are made over great distances in a north-south direction. Minor phytogeographic shifts, of the sort undergone by the beeches, are even more troublesome, for to these almost no climatic significance can safely be assigned, and they therefore tend to blur the lines between the accepted climatic zones.

Until an absolute chronology is available, however, the pollen chronology must be used as the best we have for postglacial events. Moreover, it is possible (Deevey, 1939) that, if the climatic optimum was the result of extraterrestrial causes, events related to it may have been contemporaneous in the astronomic as well as the pollen-analytic sense.

TABLE 8.—DIAGRAMMATIC CONCEPTION OF PHYTOGEOGRAPHIC MOVEMENTS OF BEECH, HEMLOCK, AND HICKORY IN THE EASTERN UNITED STATES SINCE THE IMMIGRATION OF DECIDUOUS FORESTS

ZONE	OHIO	N.J.	CONN.
C3	BEECH III	BEECH III ?	BEECH III
C2	HICKORY →	HICKORY →	HICKORY
C1	BEECH II ←	BEECH II →	BEECH II
	HEMLOCK ←	HEMLOCK →	HEMLOCK
		BEECH I	

Xerothermic Interval and Climatic Optimum.—The various phenomena referred to the "postglacial xerothermic" phase undoubtedly are in general to be assigned to *C2*. Among these in the eastern United States are the inferences, based on phytogeography without stratigraphy, that xeric coastal plain plants have found it easier to migrate inland to the Great Lakes than they do now (Peattie, 1922; Svenson, 1927) and that the prairie has left outliers in the forested regions of the middle West (Gleason, 1922; Transeau, 1935). These disjunctions are discussed in greater detail below. Whether all the phenomena of the so-called "climatic optimum" belong to *C2*, however, is another question. *C2* saw a shift from moist to dry conditions, but it is not clear that the postglacial thermal culmination corresponds everywhere to the oak or hickory maximum. "Optimum" is of course a subjective term, and, in New England, at least, it would appear that the most genial climate from the standpoint of human welfare fell in *C1*. Most of the evidence of a warmth maximum during postglacial time (warm-water marine mollusks at the site of the Boylston Street fishweir (Shimer, 1918; Johnson and others, 1942); desiccation of lakes in the Great Basin (Antevs, 1938); recession of glaciers in the Rockies (Matthes, 1939; 1940), and in Alaska (Cooper, 1942a); emerged strand lines in the Pacific (Stearns, 1945); etc. etc.), at least in North America, does not permit detailed stratigraphy. For the present we shall have to be content with extremely loose chronologic estimates of the climatic optimum, realizing that relatively warm conditions prevailed from Zone *B* to Zone *C2*, and that without pollen data in the immediate context of a supposed optimum it is impossible to be more precise. The demonstration that Littorina time began in Switzerland in 5400 B.C. (Welten, 1944) makes terminal estimates as high as 8000 or even 10,000 years not unreasonable, compared with the figures of 3000 to 5000 years usually quoted by archaeologists and others. There undoubtedly was some sort of temperature culmination corresponding to the much-debated optimum; since Raup wrote his review (1937) the whole trend of pollen data in North America has borne out the conception, and in some cases pollen of warmth-loving trees has been found in some quantity at sites now outside the range of the species—butternut and hickory have been found in Wisconsin (Wilson and Webster, 1942), and hemlock has been found on the Matamek River in Quebec (Bowman, 1931). Since Sears wrote his review of *Xerothermic Theory* (1942c) we have the demonstration that forests advanced into the tundra of southern Labrador and subsequently retreated (Wenner, 1947).

Glacial refuges.—Although it is obvious that forest trees and other non-tundra plants as well as animals must have survived repeated glaciations by contracting or shifting their ranges south of the ice margins, pollen analysis has not been very helpful in establishing the location of the refuges. In fact, as evidence accumulates that boreal forests were widely developed in the southern United States at about the climax of the last glaciation, it is becoming increasingly difficult to imagine a place where the characteristic components of the temperate flora could have taken refuge. Most striking is the discovery of macroscopic remains of white spruce, larch, and arbor vitae in Louisiana, where they are accompanied by less unexpected species such as oaks, magnolia, and tulip tree (Brown, 1938). The stratigraphic position of the fossils is not clear, but the existence of the northern species almost within sight of the Gulf of Mexico is indisputable.

The occurrence of pollen of spruce and fir is not so critical as the occurrence of wood and seeds, for it is always possible to argue that pollen is wind-borne from a distance. Still, while there are not very many pollen diagrams from beyond the glacial boundary, there are enough to indicate that spruce and fir pollen in the deeper layers is not exceptional but is a normal part of the diagram, and some of the sites are so situated that distance-transport is not a likely explanation. The available diagrams come from: western Pennsylvania and eastern Tennessee (Sears, 1935b); Cranberry Glades, West Virginia (H. C. Darlington, 1943); a North Carolina "bay" (Buell, 1945; the full diagram has not been published); buried soils in South Carolina (Cain, 1944b); and an oxbow lake in Texas (Potzger and Tharp, 1947). In addition, pollen of spruce and fir is reported from "Pleistocene" deposits in Florida (Davis

1946), though no diagram is given, and the age of the deposits is unknown. This is the full list of profiles from unglaciated eastern North America, except for that from the Dismal Swamp, Virginia (Cocke, Lewis, and Patrick, 1934), most of whose formation evidently postdates the climatic optimum, and the profiles from southern New Jersey (Potzger, 1945). The occurrence of spruce pollen in Texas is most difficult to account for on a hypothesis of long-distance transport.

The profiles from the Pine Barrens of New Jersey are remarkably uniform. Because of the presence of a little bit of nearly everything that is found elsewhere in postglacial profiles, Potzger concluded that the Pine Barrens offered a significant glacial refuge. Though any area not subject to glaciation or to a periglacial climate and not submerged under water doubtless served as a center for postglacial colonization, it seems doubtful that the Pine Barrens or any other part of the coastal plain constituted an *important* refuge for mesophytic species. Beech and hemlock pollen are practically absent from these profiles, which are dominated by pine and oak, presumably of coastal plain species, and if the lack of spruce maximum near the bottom is a reality, and not due to uninformed sampling (by the W.P.A. Peat Survey of New Jersey), the region was certainly not a refuge for spruce. The profiles are extraordinarily short, and the samples were comparatively widely spaced, so further work is necessary before they can be accepted at face value; moreover, the writer, having seen one of the localities (Martha) in company with Murray Buell and others, is inclined to believe that the whole peat section has been built up by flooding of a backwater within historic time.

By noting the order of appearance of certain genera in pollen diagrams, and by plotting on a map the sites at which a given tree appears first, second, third, etc., Sears (1941; 1942b) has attempted to locate some of the directions in which glacial refuges may have lain and to trace the course of postglacial migration (Fig. 12). This method, widely used in Europe (*see* Fig. 4, for example), also underlies the writer's remarks on the beech curve (above). Its application in North America, however, is not very successful, owing to the large number of pollen diagrams that cannot be confidently divided into zones in the present state of our knowledge, and to the danger of including incomplete diagrams. What the maps appear to show is that hemlock, oak, and beech immigrated into the glaciated area from the south, while hickory came predominantly from the west, and basswood came from a center in the northwest, presumably from the Driftless Area in Wisconsin. This last, if true, is most interesting, for the conception that the Driftless Area was an important glacial refuge has faded in popularity since the time of the early biogeographers who evidently pictured it as an island in an ice sheet, something it never was.

To summarize, the limited stratigraphic data so far obtained do not tell us very precisely where the major refuges were during Wisconsin or earlier glacial ages. We know, however, that, even so far south as Louisiana and Texas, members of the northern coniferous forest community occurred during the Pleistocene, so that, unless one can believe that the typical temperate species were pushed south of the Rio Grande and deep into peninsular Florida, the alternative is a picture of an extraordinary intermingling of boreal, temperate, and subtropical elements along the Gulf coast (and on land now submerged along that coast by a postglacial rise of sea level).

Changes of sea level in postglacial time.—Much could be and has been written on this subject, but for the most part it remains, at least in eastern North America, a strictly geologic problem; as biogeography has played little part in it, a full summary has no place in this review. The advantages of a combined attack by students of various disciplines should be obvious to anyone familiar with the European literature, but so far biologists in particular have shown little interest in the matter.

Even on a purely geologic approach it is not an easy task to investigate a rising sea level such as the one along the New England coast, for the advancing waves tend to remove or at least to drown the evidence. Studies of traces of an emerged shore line in Massachusetts and Maine (Hörner, 1929; Antevs, 1928) show that it reaches sea level a little south of Boston (although Hyyppä (1939) believes it to be above sea level in Rhode Island). This shore

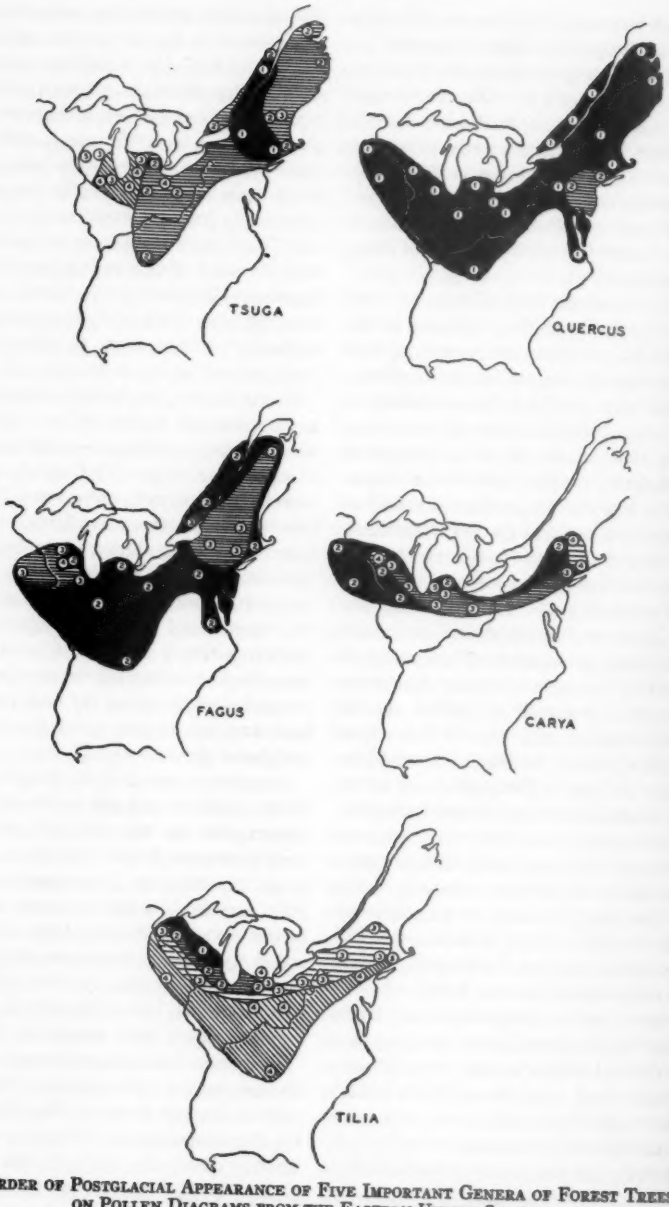


FIGURE 12.—ORDER OF POSTGLACIAL APPEARANCE OF FIVE IMPORTANT GENERA OF FOREST TREES, BASED ON POLLEN DIAGRAMS FROM THE EASTERN UNITED STATES
Redrawn from Sears (1941, Figs. 5–9).

line is believed to be of late-glacial age; its zero isobase is not a hinge line, though a hinge line for late-glacial and postglacial uplift evidently runs somewhere in the vicinity. Rathe

it marks the point where crustal recoil and the eustatic rise of sea level are in balance, and the southern portion of the late-glacial land surface is now drowned. A pollen date, now available for Oyster Pond in Falmouth, Massachusetts, where a fresh-water pond has been turned into an intermittently brackish lagoon, tells us that the rise of sea level has been going on there since *C1* time and possibly earlier. In fact the rising sea level has led to a rise of water table at inland points on Cape Cod and the near-by islands, with rather remarkable results for the vegetation as revealed by the pollen sequence (Deevey, 1948b). But a rise of sea level so late as *C1* is surely nothing but the latest part of a rise that must have begun with the glacial unloading of New England. The evidence of the earlier part of the rise, which may have been very much faster as we assume it must have been greater, lies farther seaward and has not yet come to light. At Boston (Johnson and others, 1942) the sea has risen 16 feet since the fishweir was built, and since the warm-water mollusks lived in the Bay. A pollen date of *C2* or early *C3* seems to be in order for the fishweir itself. But with such fragmentary data we are scarcely in a position to draw diagrams of the relation of land and sea during postglacial time, as Godwin does for the British Isles, for example. The magnificent material collected along the New England coast by Hyyppä will doubtless stimulate much more work on the problem by American biogeographers.

Pollen analysis in the Western United States.—The application of pollen technique to bog profiles in the Pacific Northwest has so far depended wholly on the tireless efforts of H. P. Hansen. A volume summarizing this huge amount of work has recently appeared (Hansen, 1947). For the region as a whole Hansen recognizes four phases:

IV. Cooler, Moister
III. Maximum Warmth and Dryness
II. Increasing Warmth and Dryness
I. Cool, Moist

In the establishment of this sequence Hansen has been handicapped by several circumstances peculiar to the country—its extreme topographic and climatic variability, the domination of the forest by a large number of coniferous species that are by no means ecologically equivalent, but whose pollen grains are indistinguishable,[10] and an apparent absence of postglacial climatic changes on the scale of those characteristic of western Europe and eastern North America. In the opinion of the writer Hansen has further handicapped himself by an undue reliance on absolute dates, taken considerably more confidently than their sponsors the geologists intended, or should have intended. Thus, in the extremely important matter of the use of volcanic ash horizons for correlation between mountain ranges, the relative time scale of events is first abstracted as an absolute chronology, a date being assigned to a volcanic explosion, and subsequently discovered phenomena are then fitted into the absolute sequence.

Actually, there seems to be extremely little evidence that the ash found in the Washington profiles was derived from an eruption 6000 years ago, while that derived from the destruction of Mount Mazama was laid down 10,000 years ago. The basis for the conclusion is that the Washington ash layer is related to Zone III in the pollen sequence, and Zone III, the postglacial warmth maximum, is "dated" between 4000 and 8000 years ago, while Mount Mazama pumice underlies a layer attributed to a dry interval. The danger of such a procedure is evident when we realize that Zone III is feebly or not at all developed in the Crater Lake region, where the Mount Mazama pumice occurs. Even if it were well marked, proof would be required that Zone III near Crater Lake was contemporaneous with Zone III in Washington. The dating of Zone I, from 15,000 to 20,000 years ago, inspires even less confidence, since it rests on nothing more tangible than a long-distance correlation, due primarily to Antevs, between the glacial chronology in Scandinavia and the pluvial chronology in the Great Basin.

The outstanding importance of Hansen's work consists in the demonstration that in parts of the region, notably in the Okanogan country where a pollen maximum of grassland

[10] Criticism of Hansen's method of distinguishing species of pines and spruces by the sizes of their pollen grains has been made elsewhere (Deevey, 1948a). The method as used may make it possible to record the occurrence of different species, but not to estimate their proportions in the pollen spectra.

species occurs, there was a relatively warm, dry interval during middle postglacial time. A maximum of oak pollen in the Willamette Valley seems to reflect the same climatic shift. The writer is not prepared to admit it as proved that this interval was contemporaneous with *C2* in the eastern United States, though this is a reasonable working hypothesis. In most of the Pacific Northwest the postglacial climate has been so uniform, or the vegetation has been so interfered with by volcanic eruptions whose time relations between widely separated mountain ranges are problematical, that little can be made out of the pollen sequences.[11]

Postglacial animal stratigraphy.—It is an astonishing fact, for which academic overspecialization must be held accountable, that, of all the botanists who have seen remains of microscopic animals in pollen preparations, scarcely any have attempted to identify them. Casual references to "chydorids", "Cladocera", "insect remains", and the like are numerous and especially exasperating to the zoologist scanning the pollen literature. A few workers have attempted to rectify this omission, which would have been inconceivable a century ago, but so far little of direct geographic importance has emerged.

Mollusks, of outstanding importance in the Pleistocene stratigraphy of Europe, have also been given considerable attention in interglacial and loess deposits in North America. In postglacial deposits, however, they are rarely reported, and the records come almost entirely from marl deposits of unknown age within the postglacial. As the marl usually underlies peat or a soil horizon, the molluscan fossils date from a relatively early stage in the limnological history of the basin. Wide differences in time can be expected, however, because marl is a chemically and bacterially precipitated deposit requiring a fairly high temperature for its formation (cold water can dissolve more carbon dioxide than warm, and therefore can retain more calcium in solution as bicarbonate), and the time of principal marl deposition, varying as it does with the rate of postglacial warming, is likely to be more directly dependent on the size of the basin. Thus in the small ponds in Holstein investigated by Tidelski (1929) marl deposition was largely finished by the end of the Late-Glacial, but it was shifted to the early postglacial in the Grosser Plöner See in the same region (Groschopf, 1936). When peat overlies the marl (and such sections are common in glacial landscapes underlain by calcareous drift), it reflects limnological conditions unfavorable for mollusks, and a complete postglacial sequence of molluscan faunas is not likely to be obtained with a peat borer.

Among the host of microscopic animal remains found in practically all lake and bog deposits, Cladocera are ordinarily predominant. As many as 23 species have been recognized in the deposits of Windermere by Scourfield (1943), and shorter lists from postglacial lake deposits have been presented by Messiatzev (1924), and Deevey (1942b), while several species are mentioned from Allerød layers by Gross (1937). Though such occurrences are full of interest as illuminating some aspects of the limnological history of the basins, they are too widely scattered in space to throw much light as yet on the zoogeographic history of the Cladocera. Most of the species are holarctic in distribution and are not the best of ecologic indicators, while the distribution and ecology of the others are little known. Their small size, ease of identification as fossils, and almost universal preservation in lake deposits, however, make them ideal material for the sort of statistical studies that have been made with pollen grains, and much information of direct interest to the Pleistocene geographer can be looked for from such work. Other animal microfossils of almost equal importance from this standpoint include statoblasts of fresh-water Bryozoa, which are preserved in large numbers, remains of Tendipedid (= Chironomid, midge) larvae, ostracods, mites, and sponge spicules. Tests of rhizopods, known to be common, and loricae and trophi of rotifers, which are not, will probably require special methods for their

[11] There is, perhaps, a third explanation for the uniformity of Hansen's pollen diagrams, though one shrinks from pressing it too strongly. We know that the mechanics of pollen dissemination and preservation are such as to act as an integrating machine on the surrounding vegetation, and it may be that, in a country so full of topographic and vegetational contrasts as the mountains of the West, climatic variations leading to shifts of species up and down the mountains will disappear from pollen profiles as a result of too-successful integration.

detection. Among these animal microfossils are many that may be as good temperature indicators as the plants. The bryozoan *Pectinatella magnifica* has been used in this way (Deevey, 1942b).

Southeastern United States During the Pleistocene

Biogeographic setting.—When we attempt to reconstruct conditions in eastern North America during the Pleistocene from the distribution of existing plants and animals, we are confronted with a classic problem of biogeography—the occurrence of many types in eastern North America and eastern Asia, and nowhere else. Examples among plants are the genera *Liriodendron* (tulip tree), *Liquidambar* (sweet gum), *Sassafras*, and *Mitchella* (partridge berry); parallel cases among animals are the genera *Alligator*, *Polyodon* (spoon-bill sturgeon), *Agkistrodon* (water moccasin), and the family Cryptobranchidae (hellbenders). These are not isolated examples, but particularly clear cases of disjunct distribution chosen for their familiarity to the general reader. With respect to most plant and animal groups other than birds (Mayr, 1946), eastern North America and eastern Asia have more in common with each other than they do with the opposite sides of their respective continents (Fernald, 1931; Schmidt, 1946).

There are various reasons for believing that the biogeographic connection implied by such disjunctions is old. Chief among these are the numerous instances where paleontologic evidence is available, showing that the present ranges are fragments of a formerly more continuous distribution. We know, for example, that *Alligator* lived in Wyoming in the Miocene, when the Asiatic hellbender *Megalobatrachus* lived in Europe. In the absence of such evidence the degree of taxonomic similarity proves that the connection antedated the origin of the existing species, and in some cases that of the genera. That is, eastern North America has families and genera in common with eastern Asia, and in many cases, *e.g.*, *Magnolia* among plants and *Eumeces* (skinks) among animals, the two areas together contain most or all of the species. With a few exceptions, however, such as the tulip tree, *Liriodendron tulipifera*, the skunk cabbage, *Symplocarpus foetidus*, and the Indian pipe, *Monotropa uniflora*, the species are not the same. The exceptions, which include no animals so far as the writer is aware, must be attributed to relatively low rates of evolution, and not to more recent connection. In general, then, the biota of the southeastern United States is dominated by a large number of relicts of the Arcto-Tertiary forests, which had their floristic origin in the Cretaceous, were holarctic during the early Cenozoic, and gradually withdrew into the tropics in response to slow and interrupted cooling of the nothern continents.

At first sight this whole fascinating story, admirably summarized from the botanical point of view by Cain (1944a), has little directly to do with the Pleistocene. Its implication, however, is broader than anything considered so far in this review. In the first place, Pleistocene climatic changes were more drastic than those of the earlier Cenozoic and accelerated the extinction of some stocks and the permanent withdrawal of others into the tropics. In addition, the present picture of Cenozoic climate and life suggests that the whole assemblage of species now living on the northern continents (and in the northern oceans) is of Pleistocene origin. It is difficult to see how cold-climate and cold-water stenothermal animals and plants can have arisen except under a climatic regime at least as glacial as today's. Thus for a complete view of the biogeography of the Pleistocene one should really take into account the whole sweep of Cenozoic time, and discuss such interesting questions as whether polar ice caps were in existence during nonglacial epochs.

Problems as broad as this, unfortunately cannot be properly considered here, and having recognized that they exist we shall have to be content with a nearer view of the Pleistocene. The reason for introducing the vegetational history of the Cenozoic at this point is that it seems to have been generally misinterpreted by Pleistocene biogeographers. Struck by the fact that the southern Appalachians have not been under water and not glaciated, and hence have been accessible for plants, probably since the end of the Paleozoic, various writers (Fernald for example) have supposed that the old relict genera, most of which now occur there or have

their center of existing distribution there, have lived there continuously ever since they arose. This viewpoint springs to mind naturally if one takes a view of the geologic past that regards the whole Atlantic coastal plain as "often of very modern or Quaternary origin" (Fernald, 1931, p. 27). It is very doubtful, however, whether it is a safe viewpoint to adopt in dealing with existing species. Because it assumes that all distributions of old species are themselves old unless demonstrably recent, rather than the reverse (which is the attitude of the present review), it relegates to the almost unrecoverable past problems that may in reality be Pleistocene problems. We shall have, then, to reopen the question of the suitability of the Appalachians as refuges for ancient species during glacial stages of the Pleistocene.

Blueberries, blue flags, and salamanders.—The southeastern United States, including Florida, is the home of a large number of types of peculiar distribution. Some of these, whose closest relatives are now found in eastern Asia, have been mentioned in the preceding section. Others, like the ericaceous shrub *Befaria racemosa* (Camp, 1941), have their nearest relatives in Central America or South America, and this is a pattern to which many North American bird genera conform (Mayr, 1946). Not all, however, are archaic; many are interesting merely because of more or less great disjunction. We may now examine some of the details, in an effort to see whether the persistence of peculiar organisms in this region tells us anything about the region as a glacial refuge. Some of these cases, since they involve microtaxonomy, are as interesting on methodologic grounds as for the information they bring forward, and this is the reason for discussing them in what might otherwise seem unnecessary detail.

The genus *Vaccinium* (blueberries), one of the most notoriously "difficult" of all genera, is beginning to yield to the keen eye of W. H. Camp (1942). We now realize that the chief source of the difficulty is extensive hybridization, combined with a tendency to form clones in which inbreeding is common. Apparently there are no sterility barriers between species having the same chromosome number, yet populations that seem to form "good" species are often found. Presumably they are kept apart by the patchy distribution of ecologically suitable areas (the soil must not be alkaline nor the shade too dense). A long evolutionary history in eastern North America is indicated not only by the number of basic diploid species, but by the occurrence of numerous tetraploids and some hexaploids. One of the tetraploids, *V. corymbosum*, is particularly instructive: it is mainly confined to the glaciated territory and shows evidence of synthetic formation in several ways and in no one region. The species (also tetraploids, and themselves products of a complicated history) that have contributed to the formation of *V. corymbosum* are *V. arkansanum*, now found in the Ozarks and the Mississippi Valley, *V. simulatum* of the Blue Ridge, and *V. australe* of the coastal plain.[12] Camp supposes that in pre-Pleistocene time these three species had parallel but not contiguous ranges essentially as today. The first ice advance truncated these ranges at their northern ends and led to the formation of a thoroughly mixed population when the ice sheet retreated. With repeated glaciation the northern population was so "churned" genetically that a new and highly variable species resulted. It is now separated from its ancestors by different geographic features of postglacial origin: from *arkansanum* by a wedge of prairie climate and soils, from *simulatum* by the return of dense deciduous forests, and from *australe* by the rise of sea level that has drowned the northern coastal plain.

This is no doubt an unnecessarily complicated hypothesis; presumably one glacial age would accomplish what seems to Camp to require several. However, if the separation of the ancestral tetraploids from each other was also a Pleistocene event (which Camp does not claim, believing it to have been accomplished during the later "Tertiary"), then the separation must have been the result of a glacial age earlier than the one that led to amalgamation and churning.

Thus we have the paradox that the simplest hypothesis of age requires two glacial ages to account for the facts, while Camp's more elaborate view requires only one. As the vital point at issue is the age of the tetraploids as species,

[12] The absence of distribution maps is keenly felt in reading Camp's papers, but his studies have not progressed far enough to permit their construction.

rather than the age of their distribution, it is not too much to hope that fossil evidence may ultimately be forthcoming.

The point that bears most importantly on our main problem is this: While the intermingling of species during the Wisconsin stage that led to the final synthesis of *corymbosum* could have taken place anywhere along the border of the Wisconsin ice, the fragmentation of ranges that led to the production of the older species, assuming it also to be of Pleistocene age, implies a considerable history of Pleistocene geographic changes *deep in nonglaciated territory*.

The case of *Iris versicolor* (Anderson, 1936) is also instructive. This, also, is a new species, chiefly confined to glaciated ground, whose ancestors can be pointed out with confidence. Evidence of allopolyploidy has proved invaluable here; one of the parents of *versicolor* (chromosome number 108) is *I. virginica* var. *Shrevei* (chromosome number 72), ranging from the coastal plain through the northern Appalachians and overlapping the range of *versicolor*. The other is one of the western blue flags, *I. setosa* (chromosome number 36), but close study of taxonomic characters showed that the parent could not have been the isolated eastern subspecies, *I. setosa* var. *canadensis*, but must be an unknown subspecies. This plant then turned up in the region predicted, the nonglaciated region of central Alaska, and was named *I. setosa* var. *interior*. Distribution maps of the blue flags are given in Figure 13.

Anderson reaches two conclusions of biogeographic importance: (1) that *versicolor* was synthesized when Pleistocene glaciation mingled the populations of *setosa* var. *interior* and *virginica* var. *Shrevi*, presumably along the margin of the Wisconsin ice sheet in Minnesota and North Dakota; (2) that the present ranges of *interior* and *canadensis* are relict, some populations having survived the last glacial age in the regions where they are now found. The second conclusion, so far as it is based on the distribution of *canadensis*, is an outgrowth of Fernald's nunatak hypothesis, and will be discussed below in that connection. The first conclusion is doubtless sound, but it seems not to go far enough. For one thing, one has the impression, not susceptible of proof at present, that more than one glacial age may be required to account for the remarkably great distance between the present ranges of the parent species. There is little hybridization between *versicolor* and *virginica* where their ranges overlap, partly owing to difference in time of flowering; why does *setosa* not overlap also? For another, *virginica* is itself a polyploid, and it would seem, as in the case of the tetraploid species of *Vaccinium*, that the Pleistocene history of the southeastern United States was more complicated than is implied by a simple hypothesis of amalgamation along the Wisconsin drift border.

Hairston and Pope (1948) have reported an interesting taxonomic situation with similar implications in the salamander genus *Plethodon*. Eastern North America is the headquarters for existing salamanders: 7 families, 20 genera, and 62 species occur there, whereas no other large area contains more than 3 families (Darlington, 1948). While salamanders are an archaic group, the plethodontids or lungless salamanders are highly specialized and relatively advanced. If they were originally adapted to live in mountain streams, and have subsequently become terrestrial, as herpetologists believe, their deployment in the southeastern United States implies recency of evolution, as the large number of salamander families implies a long evolutionary history for the area as a whole. Thus one may suspect that some of the genera are of Pleistocene origin, as the species almost certainly are.

The distribution of the *P. jordani* species-group (Fig. 14) is one characteristic of incipient geographic separation: three full species are recognized—*P. jordani*, *P. metcalfi*, and *P. shermani*. The last has apparently four incompletely isolated subspecies, *melaventris*, *rabunensis*, *shermani*, and *clemsonae*. Hairston and Pope believe, partly on distributional grounds, that the ancestral species is *P. yonahlossee*, though other workers have assumed it to be the widespread *P. glutinosus*. They suppose that *yonahlossee* was first separated from the prototype of *jordani* by the carving of the valley of the French Broad River, and that further isolation of *jordani* from the other two species was accomplished by similar physiographic means. *Clemsonae*, the only form found at low altitudes on the margin of the Piedmont, is regarded as a relict, though it is not clear of

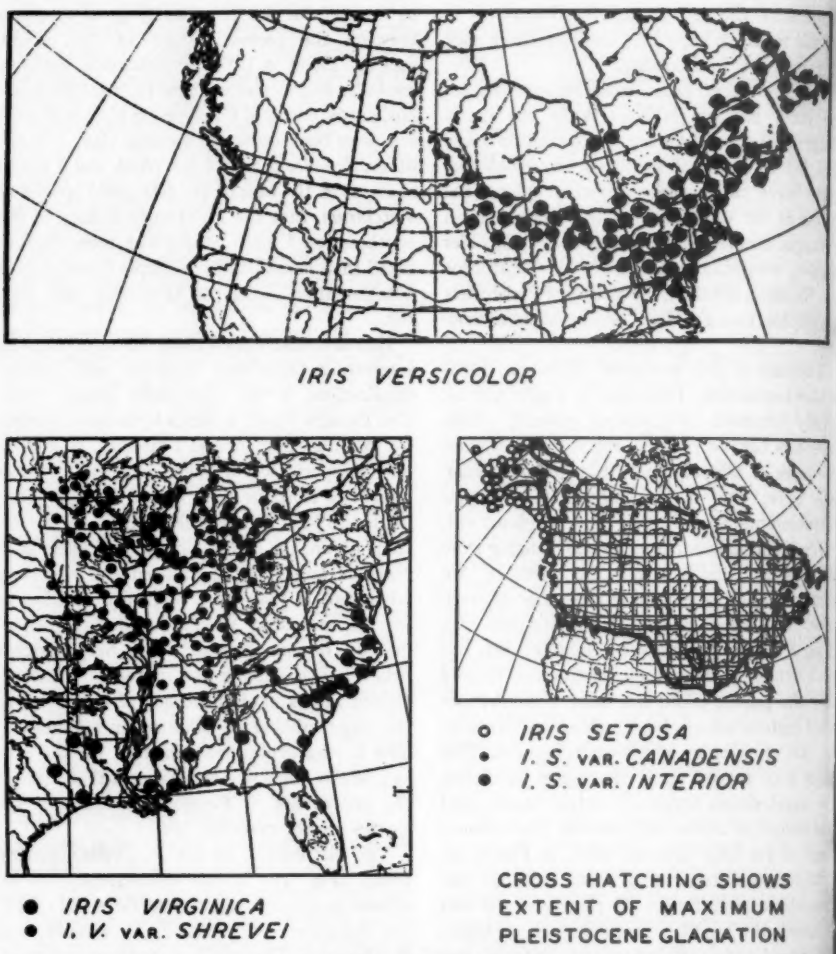


FIGURE 13.—RANGES OF *Iris setosa*, *I. virginica*, AND THE SPECIES DERIVED FROM THEM, *I. versicolor*, IN RELATION TO CONTINENTAL GLACIATION
From Anderson (1936, Maps. 1–3).

what, and its distribution is compared with that of the plant *Shortia galacifolia*. *Shortia*, however, has its other three species in eastern Asia, is a relict of the Arcto-Tertiary forest, and probably has nothing directly to do with *P. s. clemsonae*, as it is a much older species (Cain, 1944a).

It is not easy to see how species that return to streams to breed, or whose immediate ancestors have done so, can become isolated by the incision of streams into a plateau. It seems far more likely that Pleistocene climatic changes have been at work in the differentiation of the plethodontids, and that the geographic isolation required for speciation was a result of glacial chilling of the uplands where these species are now found. The complicated pattern of speciation in the genus *Desmognathus* (Hairston, 1949) certainly becomes more intelligible in the light of this hypothesis. More-

over, the distribution of *P. jordani* suggests at least two glacial ages, although, as in the cases described from the Alps, proof is lacking. If one glaciation drove the ancestral *P. glutinosus* Great Smokies in postglacial time; and (3) *metcalfi*, whose exact origin is obscure, but which could perhaps have been derived by hybridization of some *jordani* population with

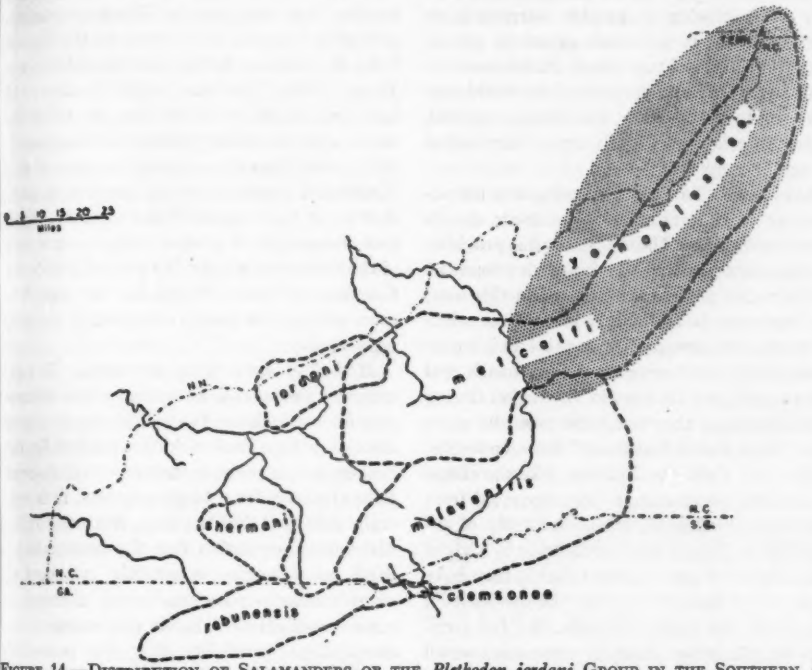


FIGURE 14.—DISTRIBUTION OF SALAMANDERS OF THE *Plethodon jordani* GROUP IN THE SOUTHERN APPALACHIANS, WITH THAT OF THE SUPPOSED ANCESTOR, *P. yonahlossee*

A third species and possible ancestor, *P. glutinosus*, is widely distributed in the eastern United States. From Hairston and Pope (1948, Fig. 11).

farther south, and gave rise to *yonahlossee* and the proto-*jordani*, the former perhaps isolated in the Piedmont, the latter in the upper Tennessee valley, one could account for the divergent opinions of taxonomists as to which species is ancestral to *jordani*. The answer, then, would be "both and neither"; the common ancestor, presumably close to *glutinosus*, is extinct. In an interglacial age both *yonahlossee* and proto-*jordani* doubtless recolonized the higher altitudes and may or may not have met in the process. A second glaciation then shattered the range of proto-*jordani*, giving rise to (1) *shermani*, which recolonized the upland from the Piedmont and differentiated in the process; (2) *jordani*, which retreated into the *glutinosus*. Some overlapping of ranges has taken place postglacially, wherever reproductive isolation had gone far enough to permit it; *metcalfi* almost fully overlaps with *yonahlossee*, but the most extensive apparent overlapping is with *glutinosus*, which however generally occurs at lower altitudes than any of the other forms except *clemsonae*. Possibly *glutinosus* has reinvaded the South since the xerothermic interval.

Such a view is of course no more than an outrageous speculation. But a theory of this kind seems to the writer at least as probable as one that supposes that populations of migratory animals are like plateau remnants, and can readily be sundered by the dissection of an upraised

peneplane. Moreover, though cases like this do not prove anything about Pleistocene climates, and though it may seem that a strict application of Occam's razor must exclude complicated hypotheses invoking the Pleistocene until existing geographic barriers have been ruled out as causative agents in speciation, what we do know about Pleistocene climatic changes in various parts of the world suggests that to consider distribution without taking them into account is unrealistic, *logical* though it may be.

Endemism.—To some biogeographers the occurrence of large numbers of endemic species in the southeastern United States has provided an argument for long-continued development of this region as a habitat. Stated in this way, the argument is certainly correct. But when the corollary is presented, that this fact is inconsistent with a picture of extensive climatic and other geographic changes in the region during the Pleistocene, then one must raise the question, "what sort of endemics?" Some endemics, *epibiotics* in Cain's terminology, like the alligator and the sweet gum, widely separated from their nearest relatives, are undoubtedly of ancient origin, though their occurrence in a given region does not prove either (a) that they have always been there, or (b) that the species itself is ancient. But other endemics, like *Iris versicolor* or *Plethodon shermani clemsonae*, which are clearly of recent origin, can certainly not be used to prove continuous existence of a stock in a uniform habitat. Rather they point in the other direction, toward the Pleistocene as a time of diversification of geographic conditions, a time when ranges were fragmented, small populations were segregated from their relatives, and new species arose as a consequence of isolation sometimes followed by hybridization. For this reason the occurrence of numerous endemics in the southeastern United States or elsewhere is meaningless from the standpoint of Pleistocene geography until the character of their endemism has been further analyzed.

Endemism in this general region has long been known among fresh-water animals, as well as among plants (Adams, 1902; 1905). For example, the fresh-water mussel genus *Quincuncina*, with several species, is restricted to the Gulf drainage in Georgia, Florida, and Alabama (Van der Schalie, 1940). Nothing is said of its affinities beyond the statement that it seems to be related anatomically to *Fusconaia* and hence "may have come originally from the west". Endemism, however, even when repeated in several genera within the same restricted locality, does not prove pre-Pleistocene origin, as is plain from the recent work on the fauna of Lake Waccamaw, North Carolina (Hubbs and Raney, 1946). This lake, at an elevation of 63 feet, and therefore under the sea when the Surry scarp was built (Yarmouth Interglacial?, Flint, 1940), has four endemic species of fish, distributed among as many families, in addition to at least one mollusk, a mussel. These endemics are not of northern origin, as are some of the interesting copepods reported from North Carolina by Coker (1938), but are related to more widespread species occurring in the same region today.

Method of overlapping inversions.—The genetics of *Drosophila*, an animal whose advantages for research are too well known to require discussion here, has yielded a method for the exploration of micro-systematics that deserves close attention from biogeographers. It is generally admitted that the large, relatively widely distributed population that the taxonomist regards as a species is actually composed of many smaller populations having different genetic constitutions. This is one source of the morphologic variability that has proved so troublesome, especially in so-called "difficult" genera. Not only may the actual genetic structure differ between populations, however, so that a given gene varies in frequency between segments of the species, but even if all genes were universally distributed through the species population we know that their linear arrangement on the chromosomes may differ. Extensive rearrangements of substantially the same genes characterize certain closely related species, such as *D. pseudoobscura* and *D. persimilis*, which are nevertheless good species usually because successful interbreeding is prevented by sterility barriers accompanying the rearrangement. Even within the species such rearrangements are now known to be extensive, and sterility barriers may be as severe between strains of the same species as they are between different species. Rearrangements arise when a piece of a chromosome is broken out and lost (*deficiency*), transferred to another chromosome

(*translocation*), or replaced in its original position after end-for-end reversal (*inversion*). A full account of this subject is given by Dobzhansky (1941).

Particularly important in this connection are repeated inversions of the same chromosome during the history of the population. When a second inversion occurs, with the breakage points coming either both inside or both outside the breakage points of the first inversion, nothing can be said about which inversion came first. But when successive inversions overlap, the sequence can be determined. Thus, considering (with Dobzhansky, p. 91) three strains in which the gene arrangements are ABCDEFGHI, AEDCBFGHI, and AEHGFBCDI, the first and second, and the second and third, are related to each other by a single inversion; either could arise from the other, and which is called "standard" and which "inverted" will depend on which was first encountered by the geneticist. But the first and the third must be related to each other only through the second, as any alternative hypothesis involves not only four simultaneous breaks instead of two, but an improbable degree of coincidence in rearrangement. The result of close study of gene arrangements, then, may be a phylogeny of chromosome construction that is extremely useful in the absence of morphologic differences among the populations. Unfortunately the phylogeny can be read in either direction, as in this example one cannot say whether the first arose from the third or the third from the first, or whether both arose from the second. However, the fact that rearrangements of this sort can occur independently in all the chromosomes will sometimes make it possible to restrict the choice among alternative phylogenies.

The method would be excessively laborious if gene arrangements could be established only by inserting mutant ("marker") genes in the stock and studying their behavior in inheritance, as was originally done. Fortunately the discovery of giant chromosomes in the salivary gland cells of the larval *Drosophila* (and some other flies) makes it unnecessary to go to such lengths, for arrangements of bands in these chromosomes are the visible counterparts of arrangements of genes. Inversions can be detected in larvae heterozygous for them by the occurrence of *loops*, configurations made necessary when homologous chromosomes pair in the region where one member of the pair is inverted.

So far the chief results of the method of overlapping inversions have been to show biologists the astonishing amount of genetic variability underlying the concept, "species", and to emphasize the importance of geographic isolation in the evolution of new species. As a device for the systematic exploration of the Pleistocene and postglacial history of a species, it has been applied primarily to *Drosophila pseudoobscura* populations in the basin-and-range country, as discussed in a later section. A certain amount of information, vague and unsatisfactory at present, but bearing on the southeastern United States, has recently come from an application of the method to populations of *D. robusta* (Carson and Stalker, 1947). This is a woodland species, whose history is presumably tied up with that of the deciduous forest in which it lives. Moreover, it is a member of a species group whose members, so far as known, are confined to the eastern United States and Japan. It is interesting, therefore, to learn that

> "If the range of the species is divided into three general regions, the northern glaciated area, the central area which has been continuously habitable to flowering plants since the Cretaceous, and the coastal plain, it will be found that, of the 14 widely-distributed arrangements, there is a median number of about 12 arrangements per locality in the central area. This may be compared to medians of 9 arrangements in localities from both the glaciated area and the coastal plain" (p. 130).

While this certainly points to the "central area" as a glacial refuge, it does not point to any particular part of the region as more favorable than another. For full use of this promising method it will be necessary to understand more about those gene arrangements that seem to be narrowly localized, and are not included in the discussion quoted above.

Persistence of plant communities on the Schooley peneplane.—In a series of papers, summarized in 1947 and in her forthcoming book, *Deciduous forests of Eastern North America*, E. Lucy Braun has argued with great skill for the view that the Pleistocene glaciations had a very limited effect on the vegetation south of the drift border. Miss Braun's opinions deserve careful consideration for they take account of the distribution of communities, to which she has devoted many years of thoughtful study, as well as the distribution of individual species. To her, as to most ecolo-

gists, the disjunct occurrence of a whole organized community is far more significant in reconstructing the history of a flora than the disjunct occurrence of a single species, which may be the result of an accident. The writer thinks this outlook, which also distinguishes the work of Gleason and Raup, for example, from that of Fernald, though highly meritorious, must be applied with caution. Its basis is the belief that an event that occurs once may be an accident, but that when it occurs many times there must be some more general explanation. But the migration of communities is more than a statistical matter, and to think of it as a concatenation of statistically improbable events may be misleading. There is abundant reason to think that in the invasion of new habitats a given species arrives when, and not until, the ecologic conditions are suitable for it. These ecologic conditions include the necessarily prior arrival of species belonging to a community of lower successional rank; they may also include the simultaneous arrival of another member of the same community. Thus, when dominant and associate species arrive together in a new region habitable for the community, the probability of their doing so is not necessarily the product of the probabilities of arrival of each species taken separately. The laws governing the migration of the community need be no more statistical than the laws governing their occurrence together in the original habitat. That the latter may also be statistical, like the laws of physics, is not denied, though ecologists are far from understanding the principles of ecologic association. The point is that, when we find integrated segments of a community in places disjunct from the main range of the community, we have to ask whether the component species could have migrated in any other fashion.

These considerations apply forcefully to Miss Braun's treatment (1937b) of the problem of coastal plain disjunctions in the interior of the Appalachians, where plants of open, dry country, including some grassland species, come largely in question. The problem is a remarkable one, as is discussed in a later section. But the occurrence together of ten coastal-plain species (Braun, 1937a) is by no means n^{10} times as remarkable as the occurrence of one of them. The same kind of argument seems to be implicit in the contention that glacial climates cannot have been very effective in the southeastern United States, because segments of communities still persist on unreduced fragments of the Schooley peneplane. In taking this position Miss Braun is following Fernald (1931), who regarded the peneplane as of Cretaceous age.

In discussing the climax-forest community of the Appalachian heartland, the *mixed mesophytic forest*, Miss Braun calls attention (1947, p. 215) to three features:

"1. The finest areas of mixed mesophytic forest occur in those places where the Schooley peneplain was never perfected, namely on the Cumberland Mountains, along the western edge of the Cumberland and southern Allegheny plateaus, and in coves of the southern Appalachians.

"2. Mixed mesophytic forest prevails over the great area where the upland levels represent the reduced Schooley peneplain, and where no later peneplain was extensively developed, that is, over the southern half or more of the unglaciated Appalachian Plateau.

"3. Relic disjunct mixed mesophytic forest communities occur almost everywhere that isolated remnants of the Schooley peneplain are found, except to the east of the Allegheny and Cumberland fronts."

When to this evidence one adds the facts (1) that many of the important species and the mixed deciduous forest itself stop at the glacial boundary, and (2) that "the mixed deciduous forest . . . is as rich in species in all layers near (not at) the glacial boundary as it is 200 miles farther south" (p. 217), one has the essence of Miss Braun's case. The last two points are of course in no way decisive. There are many ecologic factors, including those of climate as well as of soils and topography, that might give rise to a break in plant distribution at the border of the glaciated territory. As the communities of the formerly glaciated tracts must have drawn their species from glacial refuges farther south by way of a selective migration, it is to be expected that some species will not have participated in the migration, while others will have contributed to the formation of communities of different aspect on the newly occupied ground. Thus the occurrence of certain climax communities, such as the beech-maple forest, the hemlock—white pine—northern hardwood forest, and the maple-basswood forest, in the northern states and their replacement southward by floristically richer communities can tell us nothing of the character of the southeastern United States during the Pleistocene, except that the region sheltered a large pool of species

The arresting idea that these southern communities have persisted essentially unchanged since the Schooley peneplane was developed (Miocene?) is more difficult to dispose of. To the writer it seems highly unlikely, but this does not disprove it. It can be challenged, however, from two directions, as having an *internal* weakness and an *external* improbability. As to the latter, the scanty fossil evidence of Pleistocene glacial climates in the southeastern United States seems to the writer, though of course not to Miss Braun, to be against it; this is discussed further in the following section. The internal weakness, on the other hand, is apparent if we put the case like this: (1) Some species, more or less widely disjunct from their main range, are found on summits regarded as monadnocks on a Miocene erosion surface, or as belonging to a rugged country not completely base-levelled in the Miocene. (2) They belong to genera known from fossil evidence, or inferred with a high degree of probability from distributional evidence, to be old, at least as old as the Miocene. (3) Species of these old genera must have persisted somewhere in the vicinity since the Miocene. (4) There is no evidence that the existing species are not the same as the old species, or that they have a different range now from what they had in the Miocene (though the range is obviously restricted, it is restricted to part of the original whole). (5) Several of these species are known to occur together in the same small region, or in the same community, reducing the probability that any one occurrence is to be explained as an accident. Therefore, (6) these old species still occupy residual fragments of the Schooley peneplane or resistant knobs that stood above it, and have remained there while the peneplane was uplifted and dissected.

Point (2) has been sufficiently discussed elsewhere in this review, and it should be clear that the age of the genus has no bearing on the age of the species, and that the age of the species has no necessary relation to the age of its present distribution pattern, though point (3) is readily granted. Point (4) is based entirely on negative evidence. Point (5) is valid, insofar as it means that repeated occurrences of the same sort require a common explanation, but as remarked above one's astonishment need not increase by geometric progression with the number of such occurrences. Weaknesses like these are inevitable in any biogeographic argument, and it is perhaps unfair to single them out here. But if we look closely at point (1) we are entitled to ask whether all species known or suspected to be of equally great age show the same distribution pattern, or one derivable from it. The species believed to have existed on the low-lying Miocene erosion surface, in other words, ought either to be confined to residuals of that surface or to have spread out subsequently; they ought not to *avoid* peneplane remnants. But this is just what some of them do; against *Stuartia malachodendron* and *S. pentagyna*, American species of an otherwise Japanese genus, confined to Schooley remnants, we may balance *Shortia galacifolia*, confined to a low area at the inner edge of the Piedmont. Against *Buckleya distichophylla*, cited as an ancient northern outlier of a tropical family and having the required distribution in the eastern United States, we may balance the fern *Schizaea pusilla*, equally old and equally southern, but virtually confined to glaciated territory (Fernald, 1931). When we also learn (Braun, 1937b) that the remarkable colony of ten coastal-plain disjuncts on an undissected portion of the Cumberland Plateau is accompanied by northern species, elsewhere rather rare in the region, and that northern and coastal-plain plants often occur side by side, it seems that *some* of these "old" species have been selected to bolster a case, and that the case is accordingly not compelling. *On the evidence presented*, therefore, regardless of external improbability imposed by our (admittedly fragmentary) knowledge of Pleistocene climates in this region, or the inherent unlikelihood (as it seems to the writer) that plants remain on a patch of ground while the ground is uplifted by hundreds of feet and deep valleys are cut all around, Miss Braun's argument seems unacceptable. Presumably, then, certain old and certain younger species happen to occur on uplands coinciding with the unreduced parts of the Schooley peneplane simply because they find there (and nowhere else in the near vicinity) the environmental conditions suitable for them. These conditions doubtless include the rocks that have defended the remnants from erosion and the soils formed from those rocks, as well as the climatic conditions resulting from increased elevation.

How effective were glacial climates south of the

drift border.—Another line of evidence that might repay investigation in this connection is that derived from the distribution of pairs of subspecies of mammals and birds. In Europe, it will be recalled, a familiar and important pattern is a dicentric one, in which eastern or southeastern forms are separated from western or southwestern forms, not by any existing geographic barrier, but by a zone of hybridization. The presumption is, in the case of the crows, for example, that glaciation isolated fragments of the species population in southeastern and southwestern refuges, in which differentiation did not proceed long enough to keep the subspecies apart when they came into postglacial contact. Not much can be learned from this pattern, of course, beyond the obvious deduction that the central part of Europe was glaciated, *i.e.*, uninhabitable by the species during the isolation. In North America, however, where there is doubt in the minds of some that the central region was uninhabitable for many species that now live there, repetition of the same pattern might serve to dispel some of the doubt.

There is little question that the same pattern recurs in the southeastern United States, but it is not always easy to discern it in the taxonomic monographs. When a species occupies virtually the whole of North America it is likely either to be broken up into many subspecies, like the song sparrow and the fox sparrow, or else to show no systematic geographic differentiation, like the green heron and the black-crowned night heron. The latter case is perhaps less frequent than the former, certainly among mammals. But the taxonomist is no longer surprised to find differentiation into subspecies, and realizing that North America is a big and highly diversified country he is likely to look for and to find existing ecologic barriers that seem to account for the differences. Occurrence of different subspecies on the Atlantic coastal plain, in the Appalachians, in the Mississippi valley, in the Great Lakes region, etc., does not, on the face of it, call for Pleistocene isolation. That Pleistocene isolation was none the less involved is seen in certain well-analyzed cases. In the grackles, for example (Chapman, 1936; 1940), three subspecies are recognized: *Quiscalus quiscula quiscula*, the Florida grackle; *Q. q. aeneus*, the bronzed grackle of the interior, ranging from Texas to Newfoundland and to Great Slave Lake; and *Q. q. stonei*, the purple grackle occurring from South Carolina north to New York on the coastal plain and along the Appalachians. No geographic barrier separates the bronzed from the purple, but there is a zone of hybridization, quite broad in Louisiana, and in various places along the contact puzzling intermediates occur, including one called *Q. q. ridgwayi*. The purple is regarded as an offshoot from the Florida, while the bronzed would be considered a separate species were it not for the intermediates. Pleistocene isolation in refuges in Florida and Mexico is clearly indicated. This hypothesis leaves untouched the question of how the purple arose from the Florida,[13] but the main point is obvious: a species that now breeds as far north as Great Slave Lake evidently found the southeastern United States unfavorable during glacial ages of the Pleistocene, and retreated still farther south.

Another example in the *Crotalus atrox* (diamond-back rattlesnake) group is given by Gloyd (1940) and is also discussed by Mayr (1942). The Florida subspecies or species, *adamanteus*, does not come in contact with the central form, *atrox*, in the lower Mississippi Valley, though *atrox* behaves as a good species where it has come in contact with a Pacific coast form, *ruber*, in the San Diego region. There are many apparently western species that have isolated geographic representatives in Florida, including the Florida jay (*Aphelocoma caerulescens*), the Florida burrowing owl (*Speotyto cunicularia floridana*) (Chapman, 1935), and a pocket gopher (*Geomys tuza* group) (Miller, 1924), and of course there are still more species with an "eastern" and a "western" form, such as the meadowlark and the red-shafted flicker, that may or may not show intermediates along the zone of contact. In most cases of the latter sort the boundary between the two forms is the Mississippi lowland or the one hundredth meridian, and the question of Pleistocene isolation in separate refuges accordingly does not arise. But it is particularly instructive to learn that conies (*Ochotona*), now confined to the higher peaks of western North America (and Asia), are known from Pleistocene deposits in Pennsylvania and Virginia (Hay, 1923). If some were

[13] The speciation of the grackles is receiving further study by C. E. Huntington.

still left on Mt. Washington, we should see at a glance that North America and Europe are essentially alike in their dicentric pattern.

It appears, then, that the scanty information we have from fossils showing the climatic character of the southeastern United States during glacial ages of the Pleistocene, and the much more copious data on the modern biogeography of the same region, are not in conflict. We know that white spruce, larch, and arbor vitae grew near the Gulf coast in Louisiana, and that the walrus occurred as far south as Charleston, South Carolina (Hay, 1923). We know that pollen diagrams from nonglaciated Pennsylvania to Texas, few though they are, invariably show spruce and fir at their bases. From modern biogeography, without stratigraphic data, we know that there are "northern disjuncts" not only along the Appalachian chain (such as the fir, *Abies fraseri*) but in the Deep South (such as the yew, *Taxus floridana*, on the Appalachicola River bluffs in northern Florida (Braun, 1947), and the staghorn sumac, *Rhus typhina* (Brown, 1938) in the Tunica Hills of Louisiana. If one admits, with Miss Braun, only "slightly cooler climates, [as well as] lack of competition on newly exposed Pleistocene coastal terraces and on fluviatile deposits" (1947, p. 216), to account for the northern infiltration, another difficulty arises. Cooling sufficient to permit the growth of spruce and fir forests on the summits of the Appalachians should have wiped out the remarkable relicts of the Miocene flora, some of which now occur on some of the same summits. In other words, the cooling must have been more than "slight", at least during one glacial age. It is undeniable that during interglacial ages conditions at least as warm as today must have prevailed throughout this region, and even during glacial ages it is not argued that tundra conditions held sway along the Gulf of Mexico, or that climatic zones and their accompanying biota marched and countermarched with military precision from Mexico to Canada. The Pleistocene deposits of Louisiana also contain tulip tree, sweet gum, tupelo, and magnolia along with the northern conifers, and an analogous mixture characterizes the mollusks (Richards, 1938). Such a mixture implies a lessening of seasonal climatic differences, the summers in Louisiana being cool enough for spruces while the winters were still warm enough for magnolias. But taking all the facts together it seems to the writer that glacial chilling in the southeastern States must have been fairly extensive, and that the warmth-loving species, including many or perhaps most of the "Miocene relicts", survived in peninsular Florida and in Mexico, and have subsequently migrated to their present localities.

Glaciated Eastern North America During the Pleistocene

Northern relicts.—Whatever one thinks of the Darwinian notion of glacial refuges and postglacial expansion as applied to nonglaciated regions, such as the southeastern United States, there is little disagreement as to its essential correctness for the glaciated territory. The retreat of the ice sheets from south to north must have been accompanied by a re-expansion of species to "seize on the cleared and thawed ground," and, while some of the tundra forms of the first wave of migration are now confined to the Arctic regions, others have been stranded on the tops of high mountains and in other "northern types" of habitat, resulting in the familiar arctic-alpine or boreo-alpine distribution pattern. Boreal relicts are well known from the alpine zone of Mt. Washington (Antevs, 1932), Mt. Marcy (Adams and others, 1920), and other high mountains of the eastern States, and it is customary to find species whose main range is in the northern States and southern Canada sending a long tongue down the Appalachian chain at comparatively high altitudes. Of course northern relicts occur even farther south: beeches are found in the highlands of Mexico and Guatemala (Sharp, 1946), as are species (*exannulatus* and *aduncus*) of the boreo-alpine moss genus *Drepanocladus* (Wynne, 1944), while crossbills live in what are essentially patches of northern coniferous forest in the upper ranges of Hispaniola (Wetmore and Swales, 1931; Marie-Victorin, 1943). Still farther south, in the Chilean cordillera, are a few outliers of clearly northern genera, such as the crowberry, *Empetrum*, a *Drepanocladus* (*D. uncinatus*), and a few others (Cain, 1944a), giving the *bipolar* pattern that is generally found within a genus rather than within a species, and that is commoner among plants than among terrestrial animals (Berg, 1933). These are extreme, rare, and highly interesting

examples of a situation so familiar in the northern States as almost to escape notice. The farther north one goes, in other words, the more the biota is dominated by "northern relicts," but, as the degree of possible disjunction necessarily diminishes, a given species becomes less likely to be thought of as a relict. Thus the taxonomic monographs will list without comment as occurring in "Connecticut" a species known only from peat bogs at high altitudes in Litchfield County, and whose nearest stations are in northern Massachusetts.

Northern relicts are particularly banal in the fresh-water fauna of the northern States—*i.e.*, the States to which deep lakes are largely restricted because of absence of glaciated terrain elsewhere. The hypolimnion of nearly every lake in eastern North America with a mean depth greater than about 50 meters provides a refuge for northern stenothermal species that has persisted virtually unmodified since late-glacial time. In the absence of lakes comparable to the Alpenrandseen, situated far south of the Scandinavian Ice Sheet in central Europe, the disjunctions in the North American fresh-water fauna are not so spectacular and the number of species involved is smaller; moreover there is less temptation to suppose that some of the species may have survived *in situ* during one or more glacial ages. However, just as in Europe (summary in Zschokke, 1900), there are many crustaceans, turbellarians, insects, and coregonid and salmonid fishes that are widely distributed in the arctic and subarctic regions and that are of more or less disjunct occurrence in the northern United States. Some of these also show clear evidence of direct marine origin; their distribution here proves the point, rather difficult to prove in Europe, that though the species is doubtless descended from marine ancestors living in late-glacial seas that were gradually transformed to fresh-water lakes, it is now a fresh-water species and has been able to migrate postglacially. *Pontoporeia hoyi* and *Mysis relicta* dominate the deep-water crustacean fauna of all the Great Lakes and are not confined to lakes that are genetic descendants of the Champlain Sea, while *Mysis* now occurs in Green Lake and Trout Lake, Wisconsin. Some of these species, land-locked perhaps since late-glacial time but in lakes that were certainly *not* arms of a late-glacial sea, have given rise to endemics, *e.g.*, the Sebago Lake (Maine) salmon, *Salmo salar sebago*. Unfortunately, though these facts and many others like them are well known to limnologists, there is no summary of them from the point of view of the Pleistocene.

The occurrence of northern relicts is only part of the story of the influence of glaciation on the biota of the glaciated territory. The topographic diversification of habitats, or in some instances the mere opportunity to colonize unoccupied ground, has permitted the development of many species that are largely or exclusively confined to regions formerly covered by ice sheets.

P. J. Darlington (1943) gives a good example in the carabid beetle *Patrobus fossifrons*, one of those carabids that are polymorphic in respect to presence of wings. The ancestral subspecies (± winged) occurs along the west coast from Alaska to California. A − winged form is found on some of the large Alaskan islands, while the + winged subspecies has invaded the glaciated country from Alaska to the Gulf of St. Lawrence. In plants it has often been claimed that polyploid species are particularly well represented in glaciated districts (Cain, 1944a, Chapter 29; Camp and Gilly, 1943). In animals species formation by polyploidy has been generally regarded as extremely uncommon. However, recent work of Svärdson (1945) on the salmonid fishes indicates that this opinion will probably have to be revised. There is good evidence that the Scandinavian salmonids form a polyploid series, and Pleistocene commingling of ranges and the formation of hybrid swarms are called upon, as so often in plants, to account for this remarkable fact. Examples of Pleistocene formation of polyploid species and their occurrence in glaciated regions have already been given in *Iris versicolor* and *Vaccinium corymbosum*. Examples of mollusk species, not known or believed to be polyploids, but evidently the result of postglacial radiation in new habitats on the part of a single old species, are discussed by Baker (1930).

Another result of glaciation has been the formation of "semi-species," taxonomic groupings containing forms that behave as subspecies in one context and as species in another. These complexes evidently owe their origin to isolation in glacial refuges, followed by postglacial re-

expansion with some overlapping of ranges, as discussed recently by Rand (1948). The familiar case of the European crows has been almost everywhere in the glaciated northern States and southern Canada, but are moderately well known. The biogeographic problems

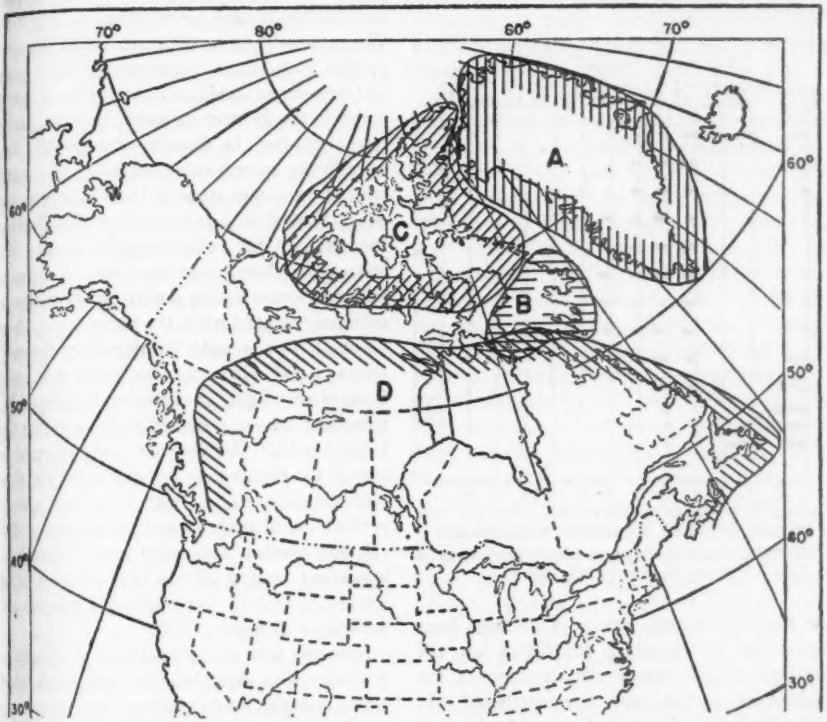


FIGURE 15.—BREEDING RANGES OF GULLS OF THE *Larus leucopterus-argentatus* COMPLEX IN NORTHERN AMERICA

The Iceland gull (*leucopterus*, A), Kumlien's gull (*kumlieni*, B), and Thayer's gull (*thayeri*, C) behave to each other as subspecies, while the herring gull (*argentatus smithsonianus*, D) seems to be a subspecies of *thayeri*, but behaves as a full species where it overlaps the range of *kumlieni*. It is supposed that isolation in at least two Pleistocene refuges, one south of the continental ice and the other in the Arctic Archipelago, has led to incomplete speciation in this case. From Rand (1948, Fig. 3).

presented in the preceding chapter; a North American example is given in Figure 15.

Peat bogs.—Interesting though they are in connection with northern relicts, the higher mountains of the eastern United States have been relatively little explored compared to the Alps, especially by zoologists, and the deep lakes have not been so thoroughly investigated as they deserve. The most familiar northern relicts, both animal and plant, are found in peat bogs (because they have a certain similarity to muskeg country), for peat bogs are not only common features of the landscape arising from bog studies were well discussed years ago by Transeau (1903), but two aspects of the matter require additional emphasis.

The first is that not all bogs occur in the glaciated districts, though most of them do, and the more southern bogs of the coastal plain do not all harbor northern species. For example, very near the glacial boundary, and within it in strictly coastal localities from Connecticut to Newfoundland, the bog vegetation is likely to be dominated by the coast white cedar, *Chamaecyparis thyoides*, a southern species, and not by the black spruce, *Picea mariana*. The

two may occur in the same bog, and the cedar then often seems to be winning out. Similarly the pitcher plants, *Sarracenia*, are southern species. To some workers (*e.g.* Braun, 1947)

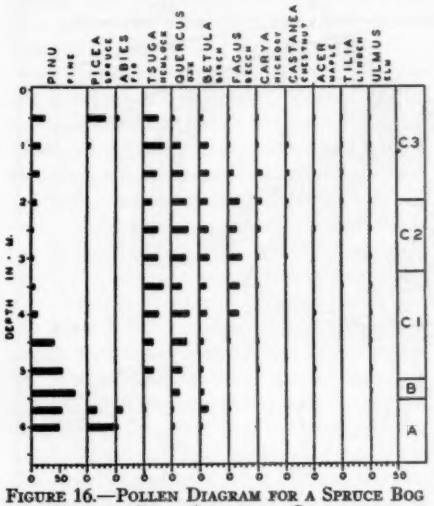


FIGURE 16.—POLLEN DIAGRAM FOR A SPRUCE BOG AT BINGHAM POND, SALISBURY, CONNECTICUT

Note the absence of spruce pollen from Zone *B* to Zone *C3*. From Deevey (1943, Fig. 11).

the lack of northern species in southern bogs argues for little northern infiltration into the southern States during glacial ages of the Pleistocene. But it must be remembered that ice is also lacking from the northern basins that formerly contained it, *i.e.*, that much has happened since the climax of the last glacial age. As we know that southern species have invaded bogs in glaciated country where postglacial conditions have favored them, stratigraphic evidence is necessary before one can say that their invasion of southern bogs is not also postglacial.

The second point is that though bogs are relict habitats and now shelter relict species, the species have not necessarily lived in the habitats continuously since late-glacial or early postglacial time. The majority of American bogs that have been investigated stratigraphically, among them those whose depths were plumbed by Thoreau (Deevey, 1942a), began their life as ordinary lakes, without floating mats or other evidence of excessive deposition of organic matter, and could not have been suitable for the extensive stands of spruce and larch that now live around them. The pollen diagrams, too, often show that spruces have only recently begun to return, partly for climatic reasons, after an absence lasting since Zone *A* (Fig. 16). Where were they in the meanwhile? As other profiles in the same region usually show traces and sometimes significant quantities, of spruce pollen in the intervening zones, they can hardly have retreated to Canada. Presumably they were living around other lakes, which became bogs at an earlier stage of their existence, and which have since become extinct. But then the spruces, and the other northern species that accompany them, must have been doing more moving around during postglacial time than is ordinarily implied when the botanist calls them "relict." This simple stratigraphic discovery seems to put relicts of other kinds in a whole flood of new light. It shows that disjunct distributions are not necessarily old, and that the habitat which shelters the disjuncts now is merely the closest they can get to the one they prefer, or the one in which they have a competitive advantage against more widely distributed species. This point has an extremely important bearing on the next problem to be discussed, that of the celebrated *nunatak hypothesis* of Fernald (1925).

Survivals from interglacial ages: Nunatak hypothesis.—The view that the whole of glaciated North America (and of Europe) was completely sterilized by glaciation, and that all species now found in these regions have reached their present localities in postglacial time, is sometimes referred to (usually contemptuously) as the *tabula rasa* theory. Against this view, which certainly goes too far, numerous objections have been raised. Prominent among its opponents, as we have seen in the last chapter, are (1) those who follow the Irish argument to its logical conclusion (Scharff, Praeger), (2) students of the Scandinavian mountain flora (Nordhagen, Dahl), and (3) those who believe, on various grounds, that some parts of the fauna and flora of Greenland, Iceland, the Faeroes, etc., have survived there since before the last glacial age (Ostenfeld, Lindroth). In North America, too, this opposition has been vociferous, and has also taken various forms.

In its mildest manifestation, perhaps, we have the interesting thesis of Miss Braun (1928,

that there are survivals from Yarmouth time still living in their original habitats in Ohio. The argument is as follows: South of the limit of Illinoian drift there are patches of a xerophytic (*Andropogon scoparius–Bouteloua*) type of prairie community, containing no western elements, but instead coastal-plain elements such as *Agave virginica* and *Ophioglossum Engelmanni*. These are quite unlike the patches of "prairie peninsula" (Gleason, 1922), which are more mesophytic and contain many western species (regarded as relicts of an eastward extension of prairie during *C2* time). One patch occupies the top of a rock that was cut off by an Illinoian stream. The Illinoian till plain to the north contains hygrophytic boreal relicts, considered to have persisted there since just after the Illinoian deglaciation. Since they held the ground, spreading of the xerophytic prairie from the area of Wisconsin till was precluded in pre-Wisconsin as well as post-Wisconsin time. The patches must then be northwestern outliers of pre-Illinoian vegetation, preserved because of their isolated position above the level of Illinoian stream erosion.

Because it contains two unproved and improbable assumptions, this hypothesis seems doubly unlikely. (1) Why should the hygrophytic boreal relicts be post-Illinoian, and not post-Wisconsin? The Illinoian till plain is so close to the Wisconsin boundary that if it served as a glacial refuge during Wisconsin time only boreal and arctic plants could have used it. (2) Are the powers of dispersal of these plants so limited that they could not migrate across an Illinoian stream during the whole of Sangamon time? As we have clear evidence of a migration of prairie vegetation into Ohio, and a convenient phase of postglacial time to which to assign it, a hypothesis of postglacial dispersal and restriction seems not only logically simpler but in better accord with the stratigraphic facts.

Probably because the persistence of plants south of a glacial boundary, no matter what the circumstances, is lacking in popular appeal, Miss Braun's paper has had relatively little weight, and it is not widely cited. Perhaps its chief merit is as an early instance of the careful application of the best geologic information to botanical problems, a field in which Miss Braun's influence has been pre-eminent. It is quite otherwise with the nunatak hypothesis of Fernald, for this work has been extremely productive, not only of lively discussion among botanists, geologists, and geographers of all kinds, but of much careful field research. The evidence and the conclusions are as follows (Wynne-Edwards, 1937):

At various isolated places in eastern North America there are arctic-alpine floras of peculiar character. In addition to a large group of circumboreal arctic and subarctic species (the *arctic* group), there are many others, absent from the Old World (though a few of them are Siberian) and from Greenland also, that are either typically *cordilleran* or find their closest relatives in the Cordilleran chain. For the former group a Hookerian (Darwinian) theory of glacial restriction and postglacial migration will suffice; but for the cordilleran group, because of the exceedingly localized distribution and the high proportion of endemism among its members, another explanation is required. It is thought that these species must have survived the Wisconsin age within the general region of glaciation in nonglaciated districts, including some fairly large areas (*e.g.*, the Shickshock Mountains in the Gaspe and the Torngat Mountains in Labrador) as well as small peaks projecting above the continental ice sheets as *nunataks* do today in Greenland and Antarctica. There is geologic authority for the existence of these nunatak areas (Coleman, etc.), but even if there were not the extraordinary disjunction of many of these species, the apparent senescence of many of them (inferred from their apparent inability to spread), and the endemic nature of others would force us to conclude that they are older than the arctic group, and that they therefore must have survived unchanged from an earlier age.

Most of Fernald's followers would not go so far as to support the botanical evidence of survival in the face of geologic evidence of its impossibility. But a notion of this sort, applied to an area so large and so little explored geologically as eastern Canada, is not easy to uproot. In arctic and alpine regions it is notoriously difficult to find proof of overriding by an ice sheet, owing to the intensity of modern frost action and the likelihood that traces of glaciation will have been removed or covered by felsenmeer in postglacial time. Thus as one area

after another is revisited and the evidence of lack of glaciation is shown to be inadequate (*cf.* the report of Flint, Demorest, and Washburn (1942) on the Shickshocks), it is still possible for a botanist to take refuge in some other area. Moreover, if the validity of Fernald's evidence is once admitted, it is necessary to admit that there is a great deal of it, and as more comes in with each additional season of botanical exploration the botanist can imagine that he is patiently amassing ammunition against the geologist's attack.

It is clear, however, that Fernald's evidence is not valid. In the convincing paper of Wynne-Edwards (1937), who writes as an opponent, and in the thoughtful and well-illustrated article of Marie-Victorin (1938), who writes as a disaffected partisan, certain apparently unanswerable arguments are presented:

1. The distinction between "arctic" and "cordilleran" types of distribution is impossible to maintain. Cordilleran plants, which after all are New World plants because they do not occur in the Old World, often show connections between the Cordillera and eastern America by way of the Arctic. Some do not, but are isolated as at two ends of a bridge. Endemism is common in the St. Lawrence representatives of the latter group. But the circumpolar arctic plants have the same sorts of distribution in North America, including the endemism (Wynne-Edwards).

2. Many of the most celebrated local species are localized because of narrow habitat requirements, for instance the fern *Polystichum mohrioides* var. *scopulinum* that lives on serpentine, or the numerous species that live on the Mingan Islands because limestone outcrops there (Marie-Victorin; Wynne-Edwards).

3. The relict species are not confined to high altitudes, nor are all of them such species as could be expected on a nunatak. At sea level in the Gulf of St. Lawrence region, in places admitted by all to have been not only overridden by ice but submerged by the Champlain Sea, are such spectacular endemics (emphatically cordilleran in their affinities) as *Aster gaspensis*, the lady-slipper *Cypripedium passerinum*, and the thistle *Cirsium minganense*, the latter the only eastern representative of an alpine but not arctic group confined to the Rockies (Marie-Victorin). Fernald knew these facts, or others like them, *e.g.*, from Anticosti Island, and admitted that some of the relicts must have reached their present areas by postglacial migration. It was a more damaging admission than he realized (Wynne-Edwards).

4. The idea that the cordilleran plants are of great age played an important part in Fernald's thinking. Perhaps they are, but we need postulate no age greater than last interglacial to explain their disjunction, whereas the arctic species must be at least equally old to account for the obvious and generally admitted fact that they were pushed southward by an ice sheet and subsequently returned to their present localities (Wynne-Edwards). This argument is not affected by Wynne-Edwards' mistaken acceptance of certain British fossils as "preglacial," a term often used in Britain to mean "interglacial."

The cordilleran-St. Lawrence distribution pattern on which Fernald relied so heavily is well illustrated in Figure 17. It is remarkable enough; the disjunction is so great that it would not be surprising if more than one glaciation were responsible for its production. Multiple glaciation is especially likely to have been involved in the spectacular case of *Iris setosa*. (*See* Figure 13.) *I. s.* var. *canadensis*, the St. Lawrence endemic, is believed not to have contributed to the formation of *I. versicolor*. Evidently it was already isolated by the time *I. setosa* and *I. virginica* subspecies came together somewhere along the Wisconsin drift border. If *canadensis* had been present in the middle West during Wisconsin time it should have merged to some extent with other *setosa* populations. It can certainly not have survived the Wisconsin glaciation in the St. Lawrence lowland, any more than the *Cypripedium* can, so it presumably was isolated in the southeastern States. The glaciation responsible for this isolation must have been pre-Wisconsin. Probably, then, some cordilleran species are older than the last interglacial age, but this is not to say that they are older as a group than the arctic species.

The most plausible explanation for the pattern of Figure 17 is that the original range of the species stretched across the continent, as it still does in many cases, but that Pleistocene glaciation(s) disrupted it and left the remnants at either end of the "bridge" (Fig. 18). This

FIGURE 17.—DISTRIBUTION OF *Aster* (SECTION *Fulcrati*) IN NORTH AMERICA, WITH ITS UNIQUE EASTERN REPRESENTATIVE, *A. gaspensis*
From Marie-Victorin (1938, Fig. 40).

however, leaves unanswered the question, why is the pattern so asymmetrical? Were it not for the asymmetry, Fernald would not have constructed his argument as he did. It remains to be seen whether the asymmetry is all of this type, or whether the Cordillera contains outliers of predominantly eastern types. Not many examples of the latter come to mind; maples provide a case in point, and the eastern shrew genus *Blarina* is known from Pleistocene deposits in Idaho (Davis, 1939), but this problem requires a detailed investigation. In any case, asymmetries of this sort, though interesting, do not prove very much, as was shown in the case of the "American" element in the Irish biota.

In short, the evidence from disjunction, extreme localization, and marked (specific but not generic) endemism in the flora of the St. Lawrence region and elsewhere in eastern North America cannot be used to argue for survival of plants[14] there during a glacial age. However,

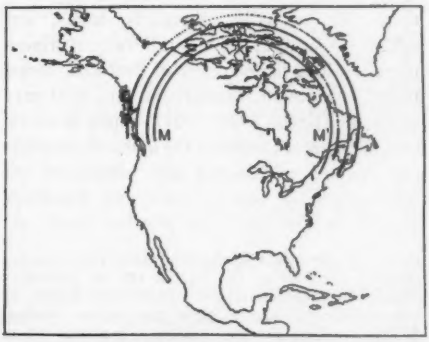


FIGURE 18.—"RAINBOW" EXPLANATION OF THE SO-CALLED *cordilleran* RELICTS IN EASTERN NORTH AMERICA

Both *arctic* and *cordilleran* plants are preglacial and interglacial species that have migrated from their high-arctic station (F) under the influence of glaciation, and the *cordilleran* plants are those that have disappeared from the Arctic, persisting at one or both ends (M and M′) of their routes. Solid lines indicate essentially continuous distribution; dotted lines mark supposed local extinction and present discontinuity. From Marie-Victorin (1938, Fig. 60).

[14] It is noteworthy that Fernald's nunatak hypothesis has been little applied to animals, and Fernald's own zoological citations were either trivial or grotesquely out of date. Eaton (1933/1934) claims that the failure of the "Laurentian" colony of herring gulls to migrate regularly, while Great Lakes gulls migrate in accordance with the old glacial

in destroying Fernald's case we must be careful not to destroy too much. Ostenfeld (1926) mentions 54 species of vascular plants that have actually been found growing on nunataks in southwestern Greenland. Of these, although the majority are of course arctic and high-arctic species, a remarkably high percentage (20.4%) are not mainly arctic, but boreal in their distribution. Eight species (not named by Ostenfeld), of which three are high-arctic and five arctic, were taken on a nunatak on the north coast (about latitude 81° N.) by the Second Thule Expedition. Several species known from the St. Lawrence region and from high altitudes in northern Labrador also occur on nunataks in Greenland (Abbe, 1936); among these are *Luzula confusa*, *Silene acaulis*, *Saxifraga oppositifolia*, and *Salix herbacea*. Fifteen species were collected on Mt. Bertha in the Fairweather Range in Alaska (Cooper, 1942b). This mountain, though not precisely a nunatak today, must have been one a few centuries ago, before the glaciers retreated. Again a considerable number of the plants are ordinarily of boreal rather than arctic distribution. As for animals, there is also no question that some forms occur today on nunataks; on dry land these are primarily springtails, mites, and spiders (Steinböck, 1939), but if water is present there is a long list of rhizopod Protozoa, nematodes, crustaceans, tardigrades, etc., that may be found (Kreis, 1920; 1921). There is no essential difference between the fauna of nunataks and that of neighboring high mountains not surrounded by eternal snow, as Steinböck showed in the Alps; the hardiest forms are selected, and they are usually species of very wide arctic-alpine distribution. The point is none the less clear: if nunataks rose above the continental ice sheets in Europe and North America, we know species that could have survived on them. Conversely, the arctic and high-arctic flora and fauna of the present day doubtless contain many species that lived through one or more glacial ages on various nunataks. It does not follow, of course, that any of them survived *exclusively* on nunataks instead of south of the ice sheets.

Is postglacial migration still going on?—Various workers, seeking to understand present distributions of animals and plants in terms of postglacial re-expansions of range, have pointed to changes within historic time as examples of the continuation of this process. There is, naturally, a great deal of this kind of evidence, but owing to the universal disturbance of normal habitats by various sorts of human interference it must be used with extreme circumspection, if at all. Moreover, it would be difficult or impossible to obtain a clear picture of faunistic and floristic changes even in virtually undisturbed areas, for the changes, like the climatic fluctuations that usually underlie them, do not point in any one direction for any large area. The evidence is reasonably consistent that the mean temperature of arctic regions has been rising since about the middle of the last century (Weickmann, 1942), and the influence of this trend on the distribution of marine fishes has been summarized by Berg (1935). There is however, great controversy over the question whether the arctic timber line is advancing or retreating, and it would seem that it is probably stationary or advancing in some regions and retreating in others (Griggs, 1946). Kalela (1940) has shown particularly clearly that before 1940 the polecat, *Mustela putorius*, was extending its range into Finland from the east. Presumably this was in correlation with the general trend toward increasingly warm winters, as both warm winters and polecats have been less conspicuous since 1940 (Kalela, 1948). But there is no reason to believe that the same zoogeographic change has been occurring in Scandinavia, although the polecat has been known there since Boreal (Ancylus Lake) time. Many water birds of predominantly southern or eastern distribu-

theory of the origin of the migratory trait, implies survival through an Ice Age in the St. Lawrence region. In this case Eaton's facts were faulty, as later studies of banded gulls have shown (Gross, 1940). It is not the only instance, however, where features so tenuous as migration routes have been believed to reflect past geographic conditions: witness the recent claim (Wolfson, 1948) that the famous migration of the arctic tern argues for continental drift. This theory is discussed by Amadon (1948). A similar suggestion was advanced as soon as the life histories of the European and American eels were known (Von Ubisch, 1924; Willmott, 1930; *see* also Ekman, 1933a). For an opinion that various birds, in migrating north across the Gulf of Mexico, do not land until they pass over the part of the coastal plain that was submerged during glacial ages of the Pleistocene, *see* Lowery (1945); also a paper by Williams (1945) claiming that the evidence that birds do in fact cross the Gulf in appreciable numbers is inadequate.

tion have also been growing commoner in Finland (Kalela, 1946; this paper contains a valuable review of the whole subject as applied to birds). But in the British Isles, where some spectacular changes in distribution have taken place during this time, notably the expansion of the fulmar petrel (Fisher and Waterston, 1941), there is no evidence that southern species in particular are involved. Consequently it would be naive to suppose that the recent expansion in eastern North America of such species as the armadillo and the opossum, has anything directly to do with postglacial climatic changes.

Another point requires emphasis in this connection. There are areas in various parts of the world that are in a permanent state of disturbance, so to speak, primitive as well as modern human inhabitants having interfered with them since time immemorial. Among such regions, termed *archaeologic disclimaxes* by Wells (1946), are certain heath areas, like the Breckland of East Anglia, the "balds" or grassy openings in the southern Appalachians, and some rather similar openings in tropical forests at moderate altitudes in Malaysia (Van Steenis, 1934–1936). Such areas often shelter rare and remarkable relicts, quite out of harmony with the general biota of the region, and thus easily lend themselves to interpretation as relict habitats, dating (for example) from times of drier climate. The implication is that post-Pleistocene invasion of species has been retarded by relatively slow physiographic evolution and soil development. In some instances the disturbance is known to be much more recent than the dry interval to whose vegetation that of the disturbed area so closely corresponds, and it is then clear, as in the case of the bogs discussed above, that relict species do not necessarily occupy relict habitats. If the species are really *pseudo-relicts* of this sort, it is obviously very dangerous to deal with changes in distribution in historic time as continuations of postglacial climatic and biogeographic trends.

As a case in point, the vegetation of certain sand plains in New England may be cited. Many kames, glacial lake beds, and other deposits of stratified drift, deposited during the shrinkage and disappearance of the Wisconsin ice sheet, today carry an open, xerophytic woodland in which pitch pine (*Pinus rigida*) stands are common. Grassland areas are not rare, while the successional stages approaching the regional climax include various oak-hickory communities. The latter especially give every indication of permanence, and Nichols (1914; 1923) regarded them as "physiographic climax." They look, in other words, very much like relict habitats dating from the oak-hickory Zone *C2*, or even from the pine Zone *B* (Table 7), and they undoubtedly shelter many of the characteristic species of those zones. In one thoroughly typical example, the North Haven sand plains along the Quinnipiac River in Connecticut, Olmsted (1937) has shown that the modern aspect is entirely the result of eighteenth century cultivation, which led to the removal of the A soil horizon and the formation of dunes, and that where attempts at cultivation have been abandoned the regional climax is being restored as rapidly as could be expected.

The North Haven sand plains are "archaeologic disclimaxes" only potentially. But such a history, and the realization that relict species have done a great deal of migrating from one "relict habitat" to another during postglacial time, entitles us to suspect some of the more celebrated occurrences of relict species. Thus in southern Ohio it is claimed (Wolfe, 1942; Transeau, 1941) that certain coastal-plain plants, widely disjunct from their nearest representatives, are still avoiding the deposits of the proglacial lakes that are supposed to have been ponded by the advancing Nebraskan ice in the upper drainage of the Teays River. (This is a preglacial river that was the ancestor of the Ohio River in southeastern Ohio and West Virginia before its diversion and fragmentation by pre-Illinoian glaciation.) The higher altitudes, apart from their content of relict coastal-plain species, are covered by the regionally appropriate mixed deciduous forest, but on the lake plains this forest is replaced by oak woodland (Braun, 1947). Before this idea, implying persistence of some elements in their present habitats since before the Pleistocene, and of others since pre-Illinoian time, can be accepted, postglacial climatic changes should be ruled out, and physiographic and cultural causes for the present distribution should be investigated. Some stratigraphic information would undoubtedly be helpful.

In a sense, postglacial expansion is still pro-

ceeding, despite the fact that the climatic optimum of postglacial time seems rather generally to have been passed, particularly in northern countries. From Raup's penetrating studies of the vegetation of the Athabaska-Great Slave Lake district (1946; 1947a; 1947b) a number of approaches suggest that phytogeographic movements have persisted at least until very recently against the tendency toward climatic deterioration. First, such studies have to be looked at against the broader background of Hultén's researches (1937).

According to Hultén, distribution patterns of boreal and arctic plants are themselves reducible to a pattern, so that a group of species (*radiants*) has a *center* and an *equiformal progressive area* of dispersal. The principal centra discernible in the ranges of hundreds of boreal-arctic species all turn out to be located in regions that were not glaciated during the maximum advance of the ice sheets. They are: northeastern Siberia, the Amur-Manchurian region, the Altai-Sajan region, the northern shores of the Bering Sea, the Yukon valley, the Arctic archipelago, and the Washington coast. These centra are believed to have served as refuges during the last glaciation, but the postglacial reoccupation of previous ranges has not proceeded at equal rates, in part because plants confined to small refuges have been depauperated of biotypes through the Sewell Wright effect. Depauperate species are less plastic and are presumed to spread less rapidly; this accounts for the phenomenon regarded as "senescence" by Fernald and others.

Raup (1947a; 1947b) has applied Hultén's methods and concepts in detail to some segments of his Mackenzie flora; he finds that despite a number of necessary modifications in the treatment of particular species the hypothesis stands up under rigorous testing. The first plants to reach the Mackenzie Mountains should have been the wide-ranging Arctic-Montane species derived from at least two of the adjacent centra—the Yukon valley and the arctic lowland—, as well as from refuges south of the ice in America. Next should have come the Continental West American radiants, mostly from the Yukon and the northern Rocky Mountains. The species derived from Beringian centra should be poorly represented, because these species suffered biotype depauperization, and the American coast radiants, primarily species of moist climates, should have had great difficulty in spreading so far inland as the Mackenzie country. These considerations are borne out by analysis, whether or not Hultén's grouping is taken as the starting point. The flora as a whole is impoverished in comparison with that of other arctic regions, presumably reflecting remoteness from the centra as well as the continentality of the climate. Postglacial recolonization, then, is presumably still taking place.

Raup (1946) emphasized that the Mackenzie district is a meeting place of eastern and western species pairs, whose formation evidently dates from glacial separation of ranges into southeastern and southwestern components. Examples of this familiar pattern can be arranged in a series; among the dominant tree species the least mesophytic types, the spruces, which occupy the farthest outposts of forest in the region, seem to have gone furthest in the intermingling of types, the eastern *Picea glauca* and the western *P. g.* var *albertiana* forming intermediates on a broad front. To a lesser extent this is true of the eastern jack (*Pinus banksiana*) and western lodgepole (*P. contorta*) pines, whose ranges overlap only slightly, while

> "the eastern and western firs (*Abies balsamea* and *A. lasiocarpa*) have not joined their ranges at all, although they apparently have come near doing so in central Alberta. Other still more southern pairs such as the hemlocks and arborvitaes are yet far apart, and are not represented at all" (1946, p. 74).

Similar cases of isolation and subsequent expansion of bird species are discussed by Rand (1948).

A third line of evidence is more conjectural, because it involves the time relations of glacial retreat and forest advance in the northern interior plains. In an area all of whose soils are youthful it is still possible to show differences in age of land surface that are reflected in the composition of the vegetation, though of course other factors are also involved. The oldest land surfaces, above the highest (1600-foot) proglacial lake, are occupied by black spruce and lodgepole pine, while the youngest, the modern flood plains below the shores of the latest (700-foot) lake, are dominated by white spruce.

It is remarkable that the numerous sections cut by streams in the older lake deposits show no trace of the enormous quantities of driftwood now being carried by the Mackenzie and its tributaries, whereas this material is abundantly preserved in the youngest stratified drift. Evidently

> "the Peace, Athabaska, and their tributaries were not flowing through a timbered country until after the last ice had disappeared from Athabaska and Great Slave Lakes, and until after the lakes had nearly reached their present levels" (p. 77).

If Antevs (1931) is right in believing that the last ice did not leave the Keewatin and Labrador regions until 7500 to 9000 years ago, and if a relatively long tundra phase preceded the immigration of forests, the age of this immigration falls close to that of the climatic optimum, and there would be no reason to suppose that postglacial recolonization has ceased.

This whole story, for the documentation of which stratigraphic evidence is sadly missed, reminds one forcibly of the oft-cited fact that many species have extended their ranges up to but not upon the moraines of the last ice sheets. Certain birds appear still to be avoiding the area of the Scandinavian Ice Sheet in Finland (Palmgren, 1938). Surely what they are avoiding is plant communities characteristic of relatively youthful topography and soils, and, when the landscape matures and the appropriate plant communities become established, the birds will follow. In this sense the postglacial extension of range is undoubtedly still going on, but this is not a sense that permits us to operate with observed changes of range within historic time and to draw inferences from them.

Xerothermic Interval.—That postglacial time in glaciated eastern North America has seen at least one episode of climate warmer and drier than today is clear from pollen diagrams. Zone *C2*, generally characterized everywhere east of the Lake States either by a rise of hickories or of oaks at the expense of more mesophytic trees, would appear to meet the requirements of a "climatic optimum," so far as higher temperature can be regarded as optimal. The climatic optimum, however, is a more vaguely defined phenomenon and ought not to be restricted to the oak-hickory zone when stratigraphic data are lacking. More generally speaking it corresponds to the warm phase of middle postglacial time, the "warm period" of Von Post (1946) and the "altithermal" of Antevs (1948). As an interval that was not only warm but dry can be distinguished in North American pollen diagrams from one that was warm but moist, this *xerothermic interval* agrees more precisely, in character if not in age, with the Sub-Boreal of Blytt and Sernander.

Knowledge of the existence of such an interval, however, antedates the stratigraphic information. Various phenomena, some geologic and archaeologic as well as zoological and botanical, have been assembled under the rubric

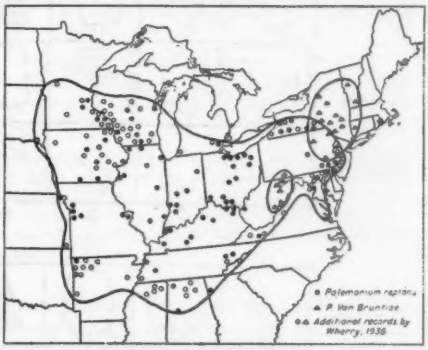


FIGURE 19.—DISTRIBUTION OF DIPLOID *Polemonium reptans* AND TETRAPLOID *P. Van Bruntiae*
It is supposed that *P. Van Bruntiae* extended its range northward in postglacial time, only to have it dissected during the xerothermic interval. From Cain (1944a, Fig. 63).

of the climatic optimum, notably by Raup (1937). The existence of such an interval was a valid inference from the facts of plant geography, and as such was clearly summarized by the great paper of Gleason (1922) on *The vegetation of the middle West*. Gleason showed that not only many plant species but segments of entire plant communities are found in Illinois, Indiana, Ohio, and even farther eastward at stations widely removed from their main ranges in the middle West. This phenomenon, known as the *prairie peninsula*, has been widely discussed, especially by Transeau (1935). The mirror image of this situation occurs in Europe, as we have seen. Isoated outliers of a western, southern, or prairie vegetation are not confined to the middle West, though their number certainly diminishes in an easterly direction.

A case of disjunction in a young tetraploid species is reported in *Polemonium* of the phlox family (Fig. 19).

The possibility cannot be ruled out that some phenomena of this sort reflect the pine Zone *B* rather than, or perhaps as well as, Zone *C2*. It seems unlikely to the writer, however, that this was a pine zone in other than the pollen-analytic sense, *i.e.*, that the climate was as dry and the pines as abundant as the frequency of pine pollen indicates. It seems more reasonable to assume that pines were only relatively abundant and to leave the climatic character of the zone for future work.

As a result of the general trend represented by Zone *C3*, we find that except for minor shifts within historic time, *e.g.*, the tendency for the climate to be a little warmer in northern countries since about the middle of the last century, the latest long-term shift of climate is one of "retrogression," *i.e.*, reversion toward cooler and more oceanic conditions. This fact underlies the whole theoretical structure by which Dansereau (1944), among others, attempts to integrate many facts of plant ecology and distribution (Fig. 20). According to this scheme, in the Gaspe region, for example (Station N 5), the patches of maple-beech forest that linger on southern slopes, in "coves," and similar protected localities are "preclimax" with respect to the regional climax, which is a northern coniferous forest type. Advancing elements of the taiga, which one finds farther northeast in Canada and which will supposedly invade the Gaspe forest if the climatic trend of the last 1000 years or so is continued, are regarded as "postclimax"; but postclimax of one station may be the climax or the preclimax of another. A paradox is involved in the nomenclature here that is difficult to explain to the geologist, for under certain circumstances the "postclimax" would be the relict of a pre-

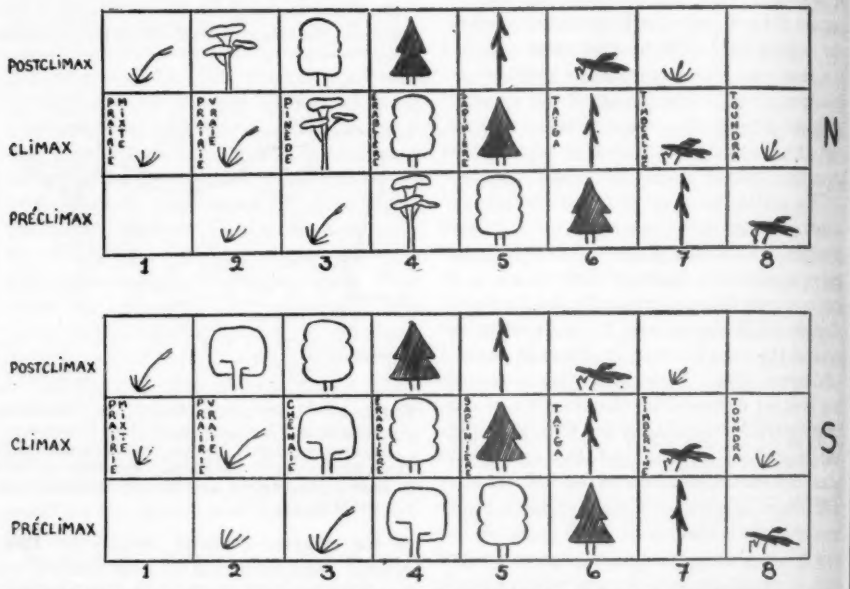


FIGURE 20.—THEORETICAL PICTURE OF THE RELATIONS OF CLIMAX, PRECLIMAX, AND POSTCLIMAX COMMUNITIES AT LOCALITIES ALONG TWO WEST-EAST (1–8) TRANSECTS, ONE NORTH (N) AND ONE SOUTH (S) OF THE GREAT LAKES

In the Gaspe region (N 5), for example, the climax forest is the northern coniferous forest (*Sapinière*), while a maple-beech-association (*érablière*), persisting in favored localities, is a relict of the xerothermic interval and has become preclimax to the regional climax. Outposts of the southward-moving *taiga*, if any, are postclimax in this locality, but climax farther to the northeast. From Dansereau (1944, Fig. 1).

existing vegetation type. Remembering that the classic example of a postclimax[11] is a fringe of cottonwood trees along a watercourse in a treeless country, the paradox is resolved as a matter of definition, but the terminology is still unfortunate.

The problem of the disjunct occurrence inland of Atlantic coastal-plain plants has already been touched on, and the opinion was expressed that this disjunction does *not* imply the persistence of lowland plants on uplifted remnants of a Cenozoic erosion surface. It seems certain that postglacial climatic changes were involved in the fragmentation of ranges of some of these plants, but it is difficult to decide which climatic shift has been mainly responsible. In the following section, the problem is treated as though the period of free migration were late-glacial or early postglacial. However, it must be remembered that it may have been during the xerothermic interval that the plants moved into the interior.

Late-glacial migration routes for plants.—For the majority of plants, including the dominant tree species of glaciated eastern North America, no particular postglacial migration route can be specified, though a careful study of pollen data may eventually throw some light on the matter. For a few species, however, notably those of coast lines, some speculations about routes of dispersal are possible and even profitable. It has long been known that the strand lines of the Great Lakes shelter species otherwise known only from beaches along the Atlantic Ocean, and in some cases, such as the rush *Eleocharis melanocarpa*, the disjunction is spectacular, from Lake Michigan to the Atlantic without a single intervening station. As Peattie (1922) realized in an important contribution to this subject, the extreme disjunctions are merely special cases, the other extreme perhaps being typified by such a common species as the cat-tail, *Typha latifolia*, which occurs on strand lines of all lakes, big and small, in eastern North America, as well as in the upper reaches of salt marshes. Many such species apparently have utilized late-glacial strand lines in their migration to interior stations, and they now occur on sandy soils derived from the shores of proglacial lakes and their outwash-

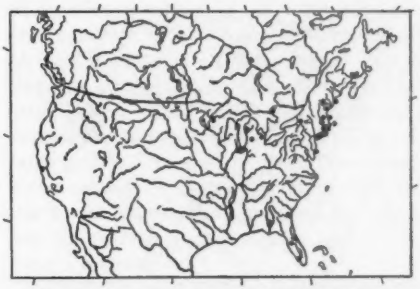


FIGURE 21.—DISTRIBUTION OF *Utricularia resupinata*, ONE OF THE SANDY BEACH PLANTS WITH AN ATLANTIC COASTAL PLAIN-GREAT LAKES DISJUNCT RANGE

Note the apparently relict stations in the vicinity of former outlets of the glacial Great Lakes, especially the Mohawk outlet of Lake Wayne, the North Bay outlet of Lake Algonquin, and the Grand River outlet of Lake Warren. Redrawn from McLaughlin (1932, Fig. 17).

choked drainage channels (McLaughlin, 1932), as well as on existing beaches. At least one species, the bladderwort *Utricularia resupinata*, looks as though it utilized the Mohawk-Hudson outlet of Lake Wayne, the North Bay-Ottawa River outlet of Lake Algonquin, and the Grand River outlet of Lake Warren (Fig. 21).

Some confusion has arisen in this problem because the strand flora of the Atlantic coast contains salt-loving and salt-tolerant as well as strictly fresh-water species. The salt-loving members are not of course found around the Great Lakes, nor are they now found around the shores of the late-glacial Champlain Sea, but some of their associates are. Svenson (1927) cleared up some of this confusion and showed that none of the salt-tolerant species are *confined* to the region of marine overlap, so that they cannot be used as indicators in the absence of geologic information.

Another sort of disjunction that has attracted some attention is exemplified by the beggar's-tick *Bidens hyperborea*, (Fig. 22). The distribution is strictly maritime in New England and eastern Canada, and then jumps to James

[11] "*Post climax:* 1. A relict of a former climax community remaining under favorable edaphic conditions in a region whose climate is no longer favorable for the development of the corresponding climax.

"2. Clements, *Plant Succession and Indicators*, 1928, p. 110—A community existing under favorable edaphic conditions and indicating the character of the climax which would be developed as the result of a climatic change involving increase in available moisture" (Carpenter, 1938).

Bay, avoiding Labrador. Most plants of this group are halophytes, but some are merly salt-tolerant, and the *Bidens* is halophobic, though confined to estuaries; no doubt its discontinuous habitat is responsible for its breaking up into numerous varieties (Cain, 1944a). Potter (1932)

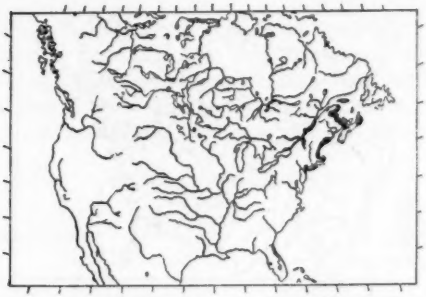


FIGURE 22.—DISTRIBUTION OF *Bidens hyperborea*, A SPECIES CONFINED TO ESTUARIES BUT LIVING ONLY AROUND FRESH WATER AT THEIR HEADS

Note the disjunct occurrence near James Bay and the absence from Labrador, implying a direct migration from the St. Lawrence valley to James Bay via a late-glacial fjord in the Temiskaming valley. Redrawn from Potter (1932, Map 11).

remarked that in late-glacial time, when the Champlain Sea or the Ottawa Sea sent a long arm up the Ottawa Valley, and there was extensive submergence around the southern part of James Bay, the possibility of migration must have been greatly increased. A marine connection between Hudson Bay and the St. Lawrence is doubtful on geologic grounds, and no stations are known for the plants in question in the intervening region. Further exploration may turn up some of the facultative halophytes in the region of Lake Abitibi, but actual marine deposits will be required to demonstrate the connection. La Rocque (1949) believes that a connection by way of Lake St. John is more likely than the one proposed by Potter.

Whether the hypothesis of late-glacial migration is reasonable depends on whether the plants are hardy enough to have followed a series of proglacial lake beaches when the lakes were in existence. In most of the cases it seems doubtful that they are. This objection applies particularly to the Great Lakes stations of coastal-plain plants, for some of Potter's species, *e.g.*, *Zannichellia palustris* and the eel grass *Zostera marina*, are not uncommon in the Arctic (Porsild, 1932) and could have lived in the Champlain Sea. The boreal species, on the other hand, though they may have used late-glacial connectives because of the sandy habitat they provided, probably did so some time after the Great Lakes had fallen more nearly to their present levels. Some of the disjunction may be due to fragmentation of ranges since the xerothermic interval.

Another possibility for coastal-plain plants was to migrate northeastward along the coastal plain itself, and many have of course done so. The suggestion that they may have found it easier to do so during a late-glacial low stand of the sea has to be taken seriously. This is a complicated problem geologically (Deevey, 1948b), but, while data are lacking for a picture of relations of land and sea in New England at any particular point in postglacial time, possibly a migration route across Georges and Browns Banks to Nova Scotia was open at some time, perhaps as late as Zone *B*. Certainly the presence of a large number of coastal-plain plants in Nova Scotia as well as New Jersey (Fernald, 1929) and the disjunction of many of them suggest that such a route was utilized, and some of the same plants have reached as far as Newfoundland, again with more or less disjunction. Nichols (1913) called attention to the fact that the coast white cedar, *Chamaecyparis thyoides*, seems to have moved directly from the tip of Long Island to eastern Connecticut and Rhode Island, while its invasion of western Connecticut was evidently later and is still incomplete. In this connection it is useful to recall that the Ipswich sparrow, a well-marked subspecies of the savannah sparrow, breeds only on Sable Island but winters with the parent species on the coastal plain from Massachusetts southward. Were Sable Island larger this situation would doubtless occur in other birds.

Late-glacial migration routes for animals.—One way in which the biogeographer can be most useful to the geologist is in tracing out former stream connections through the existing distribution of fishes and mollusks. This is a very large chapter of Pleistocene biogeography that was left out of the account of Europe and that can only be touched on here. Fish distribution in the Great Basin will be discussed in some detail in the following section, and in this

section some remarks will be made on recent work in the middle West.

It is most important for the geologist to understand that the method is fundamentally valid, though it is not always used intelligently. A sharp controversy arose between biologists and geologists on this matter, and after a period of quiescence it broke out once more (Van der Schalie, 1939; Johnson, 1941/1942). When a single species of fish or mollusk belonging to a different fauna occurs in a drainage basin, the biologist may suspect transfer by stream capture, but he is wrong in upholding such a theory in the face of geologic evidence to the contrary. The life history of fresh-water mussels includes a stage in which the larvae are parasitic on the gills of fishes, so it is unlikely that transportation of the adult mussel across the divide, *e.g.*, by birds, will result in a successful introduction and acclimation to a new fish host. It is still possible that it was the parasitized fish and not the mussel that was accidentally transported, and if the fish happens not to be a distinctive member of another fauna, or if the problem is discussed solely on the basis of mollusks and not of fish, a footless argument can easily result. Stream capture cannot be demonstrated by the occurrence of single species, but, if a whole fauna seems to be out of place, the probability of capture becomes quite high. Unfortunately the demonstration of capture by this means is easier to talk about than to perform, for distinctive species are much less numerous than widely distributed species, and they are especially uncommon in the headwater streams where capture must first take place.

The "Coosa problem" may not belong to the Pleistocene, but it is one of the most famous and controversial of such situations, and in presentation it is convenient to begin with it and to work up to the glaciated district from the south. The Coosa River is a tributary of the Alabama River, and according to an old theory based on its alignment with the part of the Tennessee River above the great bend it represents the former straight course of the Tennessee to the Gulf; the modern lower Tennessee originated later. Relationships between the mussels and crayfishes of the Alabama and Tennessee drainages were pointed out by Simpson, and seemed to support this theory, but, when D. W. Johnson found physiographic evidence against it, he proceeded to deny the validity of the biologic evidence. As Van der Schalie (1938b) has shown, there is good reason to believe that the Cahaba River in the Alabama basin has obtained many of its mollusks from the Tennessee. Not only are there seven species in common (out of about 59 in the Tennessee and 48 in the Cahaba), three of which are otherwise known *only* from the Tennessee, but there are at least seven pairs of species whose Cahaba members almost certainly came from the Tennessee. The specific differentiation implies some antiquity for the derivation, though not necessarily pre-Pleistocene origin; at any rate, though we cannot *date* the capture by this method, the case for the *occurrence* of the capture (in a direction the reverse of that required by the old theory) is strong.

On the other hand, the hypothesis of Ortmann (1913), involving extensive rearrangement of the mussel and crayfish fauna of the Appalachian region by means of headwater captures across the Allegheny divide, is unconvincing. In part this is due to grossly inadequate data; the details of distribution in this region are largely unknown. In addition there is a large amount of uncontrolled speculation that makes Ortmann's views unacceptable on methodologic grounds. Having shown that the mussel faunas on the two sides of the divide are almost entirely dissimilar, he weakened the argument by maintaining that the Atlantic slope fauna was originally derived from that of the interior. A great biogeographic trap lies before the writer rash enough to discuss matters like this, and Ortmann fell into it in an effort to determine, from the distribution of the genera, where the species came from; he thus found himself pursuing an ever-retreating subject through the reaches of the early Cenozoic and Mesozoic. That is to say, he made the fundamental and mistaken assumption that any distribution not demonstrably recent must be old. Apart from this, he failed to realize that when a species is apparently out of place the number of possible explanations is innumerable, and that if capture has taken place across divides whole segments of faunas must have been transferred. Starting from the dissimilarity between the two faunas, Ortmann examined the exceptions separately and invented

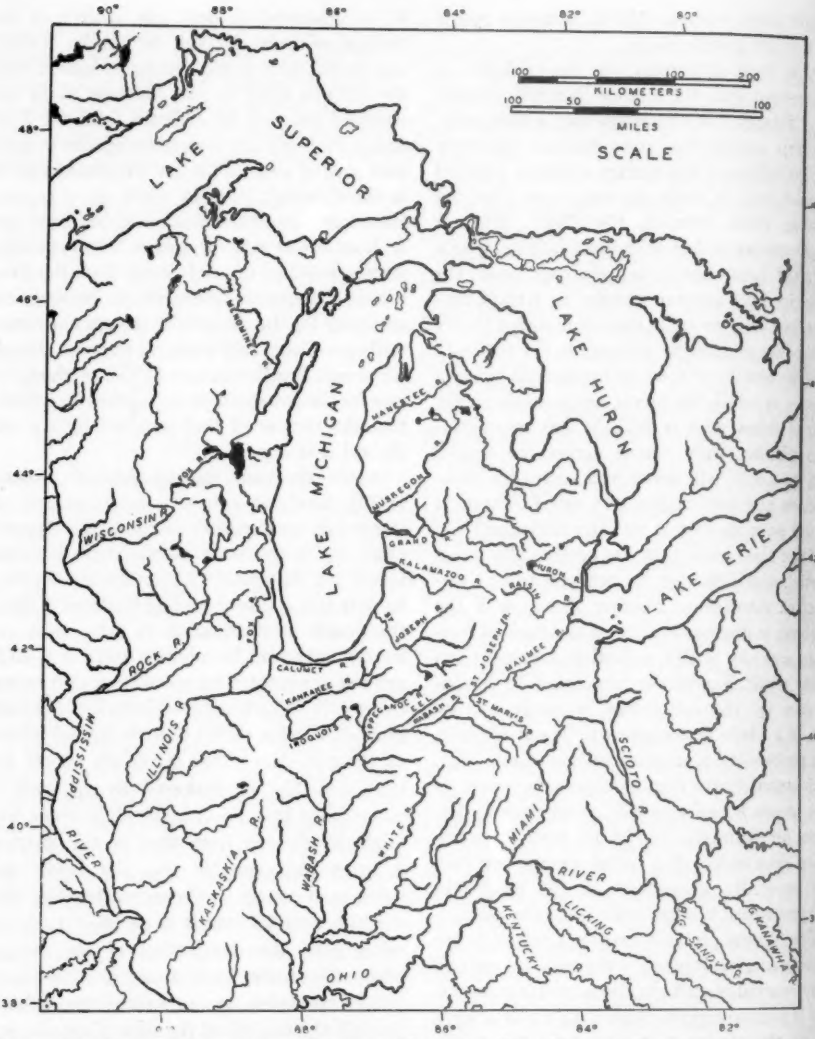


FIGURE 23.—PRESENT DRAINAGE IN PARTS OF MICHIGAN, OHIO, INDIANA, ILLINOIS, AND WISCONSIN Showing rivers mentioned in the text.

a hypothesis of capture for each of them, a different sort of capture in nearly every case.

The ease with which pseudo-problems in this field can be invented is well shown by Ortmann's discussion of the fauna of the Licking River in Kentucky. The Licking now drains to the Ohio (Fig. 23); preglacially, according to Leverett, it may have formed part of the basin of the Kentucky, Cumberland, and Tennessee rivers. Tight, on the other hand, suggested that, like the Kanawha and other branches of the modern upper Ohio, the Licking was a north-flowing stream that might have belonged to the old Erigan River system, antedating the glacial diversion that has produced the Ohio of today. According to Ortmann (1913, p. 354-355), the Licking has an Ohio fauna, and this fauna differs from that of the Tennessee and

Cumberland; therefore Tight rather than Leverett must be correct, and "this is an interesting instance, where zoogeography contributes to the solution of a physiographical question." *But the Licking still flows to the Ohio*, and its faunal similarity to the Ohio presents no real problem. The mistake is in assuming that a segment of the old Tennessee-Cumberland fauna would necessarily have been preserved unchanged since preglacial time in the modern Licking, or that its absence today proves that it never existed. There is probably no field of scholarly activity where it is so dangerous, and at the same time so tempting, to reason from negative evidence, as biogeography.

In glaciated regions we find a number of instances where fish and mollusk distributions are related, or seem to be related, to drainage modifications during the history of the Great Lakes. These cases do not all help the geologist; they are usually distributions of particular species, the explanation of which would not be apparent were it not for previous work by the physiographer. Once the value of co-operative work in this field is appreciated, however, it becomes possible for the biologist to suggest solutions not previously considered by geologists —provided always that the biologist uses his data intelligently, and does not stubbornly cling to a geologically impossible theory. It is worth while, therefore, to cite a few of these cases, chiefly in connection with Figure 23.

The great majority of fishes of the Great Lakes drainages have evidently got into the lakes by way of the Mississippi valley. Accounts of fish distribution in this region are for the most part confined to particular States: Gerking (1945) for Indiana, Greene (1935) for Wisconsin, Eddy and Surber (1943) for Minnesota. Hubbs and Lagler (1947), however, give a more general summary, and the State lists are not lacking in cross references. As an example of the use of glacial connectives by fishes, the case of the sheepshead, *Aplodinotus grunniens*, is particularly instructive (Barney, 1926). This is the only fresh-water representative of its family (Sciaenidae), an essentially southern species, which not only utilized the Illinois River and Fort Wayne outlets to colonize the Great Lakes, but must have used the River Warren to get into the Lake Agassiz drainage, for it now occurs in Lake Winnipeg and even in Lake Abitibi. It is absent from the Atlantic slope. Moreover, a fossil occurrence is known from postglacial marl in Burt Lake, Michigan, south of the Straits of Mackinac (Hubbs, 1940). Hubbs thought that the fossil might be assigned to the Lake Nipissing phase, but the penetration of the species into the Great Lakes must have been considerably earlier, as the connection with the Mississippi was broken before Nipissing time.

The earliest direct route for the penetration of Lake Erie was the Fort Wayne outlet of Lake Maumee, connecting the (now reversed) Maumee River with the upper Wabash, and hence with the Ohio. Because of later connections, first via the Imlay-Grand River outlet to Lake Chicago, and later via the Straits of Mackinac, it is difficult to say whether the Fort Wayne outlet was extensively used by aquatic organisms. At this stage or possibly even earlier, however, meltwater from the retreating Saginaw Lobe found distributaries across southern Michigan and northern Indiana to the Illinois River and Lake Chicago, and an interesting story has been made of animal distribution in this region. Wright (1932) showed on zoogeographic evidence, and supported his argument with stratigraphic data, that the upper Tippecanoe received mollusks directly from the Illinois via the Kankakee and Iroquois, and not via the Wabash and lower Tippecanoe. Four species of snails were chosen because of their modern abundance and their preservation in marl deposits, and it was shown that they all had essentially the same history though their arrivals were not simultaneous. Similarly Gerking (1947) finds that the minnow *Notropis chalybeus* is distributed "continuously" in the Kankakee and upper Tippecanoe drainages, but is absent from the lower Tippecanoe and the Wabash. This species, moreover, also occurs farther north, in the St. Joseph basin of Michigan, which was connected with the Kankakee via a now-dry channel at South Bend. Another minnow, *N. heterodon*, has a similar pattern, but also occurs in a lake in the present Maumee drainage, which it may have reached by way of an unsuspected connection between the two St. Joseph rivers.

It is curious that these species seem to have avoided the Wabash. The lower Tippecanoe evidently arose by a recent capture, for it

cuts through the Packerton moraine system while the upper Tippecanoe lies behind and parallel to the moraine. A change in ecologic conditions might explain the barrier to distribution downstream in the Tippecanoe but does not explain the apparently original absence from the Wabash. Possibly the Fort Wayne outlet was not in existence when the species reached northern Indiana, for it is thought that the Saginaw Lobe began its retreat while the Huron-Erie Lobe still occupied the basins of those lakes. It would be remarkable, however, if a species still living in Indiana were capable of approaching so closely to a large ice sheet. It seems more likely that the Wabash was uninhabitable for the species for some other reason, perhaps because it carried too much meltwater too rapidly from the Huron-Erie Lobe. In either case these examples are extremely interesting geologically, even though their meaning is not altogether clear.

Van der Schalie (1938a; 1941) contributes to this general subject some cases of mussel distribution farther north. In connection with the Grand River outlet of Lake Warren, the mussel *Actinonaias ellipsiformis* occurs in the Saginaw drainage at the Imlay end of the old channel, in the Grand, and in the St. Joseph and rivers farther south, but not in Lake Michigan, an important point, as only fluviatile species should be considered in such matters. Unlike most other Grand River species, however, this mussel is lacking from the Muskegon, though there was a late-glacial connection between the Muskegon and lower Grand via the River Rouge. This may mean "that it invaded the Grand River drainage at a period when the connection between that river and the Muskegon no longer existed, but before the severance of the confluence between the Saginaw and Grand River drainages" (1941, p. 305). On the other hand, *Lampsilis fasciola* apparently never used the Grand River outlet, for in Michigan it is confined to the Lake St. Clair-Lake Erie drainage. Van der Schalie (1938a), following Ortmann, believes that it used the Fort Wayne outlet; moreover, it is one of three species now discontinuously distributed in the Huron, Raisin, and Clinton rivers and absent from Lake Erie, a pattern that is supposed to reflect a system of tributaries to an east-flowing but longer Maumee River at a time when the Trent and Mohawk outlets were in use and Lake Erie was nearly dry. This seems more questionable.

These examples seem to require a considerable amount of migration by warm-temperate species through glacial meltwater. Stratigraphic data are inadequate to show how reasonable this may be, and there is a large field here for further research. Data from deposits of Lake Chicago, however (Baker, 1920), though in need of reworking, suggest that an essentially modern fauna and flora were established surprisingly early.

A number of species of fishes and mollusks evidently used connectives no longer existing in their invasion of Wisconsin. In fact a tabulation based on Greene's (1935) detailed consideration of the distribution of Wisconsin fishes shows that 87 species and subspecies probably used late-glacial distributaries, such as the Fox and Rock River outlets of glacial Lake Oshkosh, the St. Croix outlet of Lake Duluth, and the connections between Lake Agassiz and the Mississippi, while an additional 20 used the more southern outlets of Lakes Maumee and Chicago; 23 forms must be classified as doubtful users of at least the northern routes of dispersal and only 16 definitely did not use glacial waters.[18] Thus the discovery that the mussels of the Menominee River, now tributary to Green Bay, are those of the Wisconsin Highlands rather than of the remainder of the Upper Peninsula of Michigan (Goodrich and Van der Schalie, 1939) is not surprising; these species evidently came up from the Wisconsin River via the Fox River valley before the postglacial reversal of the Fox.

The situation in the Johnny darters is particularly interesting. *Boleosoma nigrum eulepis* is common in western Wisconsin, but also crossed into the drainage of the Fox and is present above now-impassable falls in northeastern Wisconsin. Thus it used glacial waters, and its center of redistribution was presumably in the Driftless Area. Here it doubtless differentiated in isolation from *B. n. nigrum*, which must have occupied the Mississippi Valley beyond the ice during the last glaciation. Despite the fact that *eulepis* had a more

[18] The corrections of certain distribution records by Hubbs (1945), though directed primarily to Minnesota fishes (Eddy and Surber, 1943), also affect a few of Greene's cases.

northerly refuge than *nigrum*, *nigrum* is the subspecies of northern Wisconsin, has also entered the Lake Agassiz drainage, and occurs in the Hudson Bay streams of northern Ontario and Quebec (Radforth, 1944). It appears that *nigrum* is the more agressive form in competition, no doubt because its refuge area was larger, so that *eulepis* may be said to show the "Sewell Wright effect" of biotype depletion. A third subspecies, *olmstedi*, occurs in southern Ontario and the Maritime Provinces and south to North Carolina, and clearly represents the Atlantic coastal-plain segregate of the parental population.

Following the ice sheet still farther north, Radforth (1944) gives important data on the recolonization of Ontario by fishes. For the southern part of the province nothing essentially new is provided, although the inclusion of Lakes Erie and Ontario in the account gives opportunity to discuss invasion from the Atlantic coastal-plain refuge as well as from the Mississippi valley. In the far north, however, where both the fishes and the geology are poorly known, some more obscure but highly interesting cases suggest connection between Lake Agassiz and the western part of Lake Ojibway. The goldeye, *Amphiodon alosoides* (Fig. 24), is one of the few species (the sheepshead being another) that has reached Ontario solely by way of Lake Agassiz, to judge from its absence on the Atlantic side of the divide. In addition to the range in the Lake of the Woods region, there is a widely disjunct population in the Lake Abitibi area. Similarly, *Imostoma shumardi*, the river darter, has an apparently relict outlier to the eastward in Lake Attawapiskat, and *Hiodon tergisus*, the mooneye, occurs in the Moose River drainage of James Bay. Unless these species went down the Nelson River outlet of Lake Agassiz to Hudson Bay and then back upstream to their present stiuations, which is most improbable from our present understanding of their ecology, they have been distributed across northern Ontario by late-glacial connectives that have not yet been worked out geologically. It is also of interest that at least one Atlantic-slope species, the fallfish, *Leucosomus corporalis*, has evidently crossed the divide northwest of Lake St. John, Quebec, to reach Moose River, thus failing to utilize the Temiskaming connective postulated by Potter as involved in the distribution of strand plants, but using the one recommended by La Rocque (1949).

In summary, the implication of such distribution patterns among fishes and mollusks

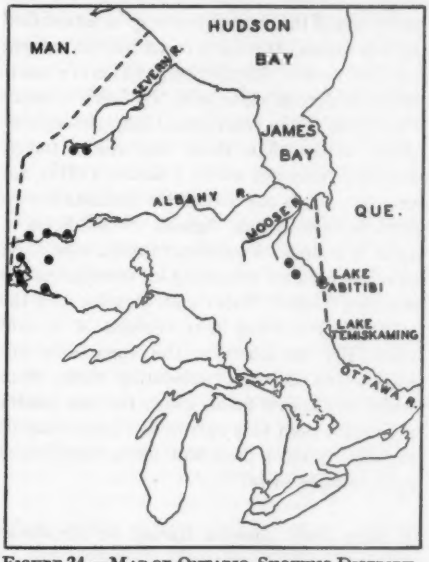


FIGURE 24.—MAP OF ONTARIO, SHOWING DISTRIBUTION OF THE GOLDEYE, *Amphiodon alosoides*

This pattern is apparently related to late-glacial connectives across Ontario from Lake Agassiz to Lake Ojibway. Redrawn from Radforth (1944, Fig. 29); there is a misprint in the legend of the original.

is most remarkable geologically. That any given species should have crossed a divide that carried water during deglaciation might not be surprising, and in fact, if its occurrence were an isolated event, a cautious biologist would presume that the crossing had taken place by some accidental means such as transportation by a water bird. But in the recolonization of the Great Lakes and their tributary watersheds there is convincing evidence of large-scale migration across regions at present impassable, for it must not be forgotten that all the Great Lakes drain to the St. Lawrence while their fauna obviously came from the Mississippi. It is the *proportion* of species that have utilized late-glacial connectives that stands out so prominently; for example only 16 out of 146 Wisconsin fishes can be shown *not* to have migrated through glacial waters. Though the evidence that some the remainder did so is

doubtless debatable, there are enough clear cases to indicate that the lakes and streams carrying glacial meltwater must have been considerably warmer than one might have supposed. Ultimately, perhaps, isotherms for various stages of the deglaciation may be established by this means. At present it can only be pointed out that modern distribution patterns of aquatic forms in general agree with the fossil evidence that parts of the great glacial lakes, though no doubt colder than their descendants today, were definitely not arctic. Coleman (1922), for example, points out that all the mollusks known from deposits of Lake Agassiz are still living in Lake Winnipeg. A subarctic tundra zone must have followed the retreating ice front across the northern United States and Canada, and the writer is convinced that remains of it will eventually be found in the apparently unfossiliferous deposits antedating those from which the known fossils come. But the tundra must have been very narrow and impermanent, and the modern flora and fauna immigrated astonishingly early.

Western North America During the Pleistocene

Larger problems.—The western part of North America, including the Cordillera, the Great Basin, the Pacific slope, and Alaska, presents Pleistocene problems significantly different from those of eastern North America. Much of this region is arid or semiarid, and there is reason to think that the aridity is in part the result of orogenic movements that have lifted mountain ranges athwart the path of moisture-laden air masses from the Pacific, the date of some of the orogeny itself being Pleistocene. Continental glaciation scarcely reached south of the Canadian border, and within the United States the story of glaciation is one of isolated ice sheets capping or spreading out from independent mountain centers, a situation that has led to the recognition of many local stratigraphic columns but little general correlation. The marine Pleistocene of California might be said to be moderately well known (Gale, 1931), but the orogenic movements introduce such a serious complication there that general agreement on correlations with Pleistocene sections elsewhere in the world may be long in coming.

Biogeographers writing on the problems of the West have had comparatively little to say about glacial climates of the Pleistocene. Küchler (1946) has discussed the remarkable poverty of the northwestern forests in broadleaf deciduous trees and attributes it to a combination of topographic and climatic peculiarities, including glaciation. Some mammalogists, notably Dalquest (1948), have seen in glaciation a powerful agent in the isolation of faunas and the formation of new species (*see also* the discussion of the origin of local variation in the bee *Hoplitis albifrons* by Michener, 1947) and have speculated extensively and interestingly on the reasons for existing ranges. It is profitable to do this now that the mammals of Washington (Dalquest) and Idaho (Davis, 1939) are moderately well known. The leading biogeographic problem of the West is, however, one of pluvial rather than glacial climates. Much can be written on this subject even from existing knowledge. However, though the present-day distribution of animals and plants would in many cases be inexplicable if we did not know that the climate of the region was more humid during certain stages of the Pleistocene, and though the biogeographer calls the attention of the geologist to these matters, the evidence is not of a nature to carry us very far. Just as we have seen it to be very difficult if not impossible to get convincing proof of multiple glaciaton in glaciated regions when we know only the present ranges of species, probably all the facts of terrestrial and fresh-water biogeography in the West could be explained on the basis of a single pluvial age. We know of course that there have been at least two major pluvials in the history of Lake Bonneville, and it is not unreasonable to expect future evidence to support a conception of three late-Pleistocene pluvial ages or subages: one is perhaps to be correlated with the Illinoian glacial stage, and the other two with the Iowan and one other Wisconsin substage. Proof of this will have to come from orthodox stratigraphy, however, and any inference of cyclic shifts from pluvial to interpluvial based on existing distribution without stratigraphic documentation can be no more than an inference.

Another matter deserves emphasis, as it points to the value of western North America as a theater of operations in obtaining the solution of certain theoretical problems posed by

the Pleistocene epoch as a whole. The evidence of pluvial climates in the Great Basin and in other semiarid regions of the world has been before the world in tangible form for at least 50 years. It would be naive, therefore, if the biogeographer should spend his entire time discussing whether or not the existence of moister Pleistocene climates is a valid deduction from existing geographic distribution. The real question is not whether pluvial ages existed, but where their influence was felt. Under a glacial climatic regime the thermal gradient between the equator and the poles must have been shorter and steeper, and storm tracks across the northern continents in middle latitudes must have taken courses far south of their present ones. Thus moisture-laden winds must have infringed on the subtropical zone of high pressure that is mainly responsible for the deserts of the world. But the belts of higher pressure cannot have been dispensed with absolutely. Neither can the whole system of pressure distribution have been displaced indefinitely southward, unless glaciation in the northern and southern hemispheres was strictly alternating and a corresponding northward displacement took place during southern-hemisphere glaciations. The latter conception is at variance with present knowledge and theory. Therefore we shall have to face the question, whether the desert barrier that now opposes the southward migration of north-temperate organisms was obliterated during the Pleistocene, or merely somewhat debilitated. That there has been biogeographic leakage into the tropics across northern-hemisphere deserts is obvious, but much remains to be done before the character of this leakage is fully understood. If all deserts, tropical as well as subtropical, were moister during the Pleistocene, organisms ought to have crossed everywhere and in all directions. If, on the other hand, desert zones were merely displaced southward, organisms should have crossed only in proportion to their pre-existing adaptations for desert conditions; in other words the limit of southward dispersal of an organism across a moistened desert should have been a function of the latitude from which it started.

On the solution of questions like this depends the ultimate correlation of glacial and pluvial ages, a matter of great concern to the geography of Africa. In Africa the utilization of biogeographic data in this problem is hampered by the long-continued existence of a water barrier between the moist-temperate and the dry subtropical zones. It is safe to suppose that only a relatively few species could pass the double hurdle, even when the climates were favorable. In North America, on the other hand, a land mass stretches continuously from glaciated high latitudes deep into the humid tropics, so that the configuration is, at least potentially, much more favorable for study than that of the Eurasiatic-African land mass.

The importance of this point, and some of the difficulties it presents, are plain when we remember that Meinzer (1922), from the study of his map of the Pleistocene lakes in the Great Basin, concluded that the driest parts of the region were about as moist during a pluvial age as the moistest parts are today—*i.e.*, that Arizona was comparable to present-day Oregon, while Oregon in turn was also much moister. Thus Meinzer maintained that the north-south gradient of moisture prevailed during the Pleistocene, while the absolute magnitudes were shifted. Much has been made of this conclusion by biogeographers such as Epling (*in* Dobzhansky and Epling, 1944), who discount the significance of the pluvial climates as factors responsible for existing ranges of species. It is a matter of the utmost importance, therefore, to learn whether Meinzer's view is valid, or whether it was based on inadequate data. So little is known of the Pleistocene geology of Mexico that the writer strongly suspects the latter to be the case. But judgment must be reserved for the present, and in the following sections attention will be mainly confined to the Great Basin itself, the larger implications being left for future research.

Fishes of the Great Basin (*See* map, Fig. 25.)—The fascination of the fishes of the Great Basin waters is not confined to the field of biogeography. When a biologist stands on the floor of a great Pleistocene lake, whose strand lines are clearly visible on the mountainsides all around him, but whose waters have shrunk until a few short streams and isolated springs are the only remaining traces of fresh water in the midst of a desert, his imagination is likely to be captured by the occurrence of a dense population of fishes and other aquatic organisms in those

FIGURE 25.—MAP OF THE PRINCIPAL DRAINAGE BASINS OF THE WESTERN UNITED STATES
Of the several independent portions of the Great Basin that may or may not have been independent during the Pleistocene, only the Death Valley system is shown separately.

waters. Knowing the importance of geographic isolation and of small breeding populations in evolution (as deduced from genetic theory), he cannot overlook the fact that a natural experiment in the mechanics of speciation has been performed for him on a colossal scale. It would be astonishing enough if any fishes had survived through a history of desiccation lasting for thousands of years; that a large proportion of the springs and streams in desert basins still harbor fishes is virtually incredible, yet it is true. Not only are populations of species small,

as for example the entire lot of *Cyprinodon diabolis*, a well-marked species, probably fluctuates between 50 and 400 annually (Miller, 1948); it is also an inevitable result of the geographic configuration that instead of a large and indifferent fauna belonging to the region, plus a few interesting but debatable relicts possibly belonging to an earlier time, ***the whole fish fauna of the Great Basin is made up of Pleistocene relicts*** (and their descendants). The implications of this fact are staggering, though they are just beginning to penetrate the consciousness of the evolutionary biologist. Possibly there are other areas whose entire fauna consists of relicts, but seldom is it possible to prove it so convincingly and dramatically.

In this review, however, we shall have to ignore the strictly biologic questions raised by the fishes of the Great Basin, and concentrate on the biogeographic aspects, to show how useful such studies can be to the geographer. The subject has recently been presented in great detail by Hubbs and Miller (1948), though incompleteness of the taxonomic work leads them to regard the monograph as no more than a progress report.

The discussion of the Lake Bonneville fauna is shorter than might have been expected. There are 12 genera, two of which are endemic (*Iotichthys* and *Snyderichthys*), 22 species, and about 28 forms in all, including subspecies. The Lake Lahontan system, no doubt because of its greater disruption since the time of its maximum expansion, has a smaller number of genera (10, one endemic) and species (13, 8 endemic) but a larger number of subspecies (about 30). Regarding connections of Lake Bonneville with adjacent basins, there are obscure indications that some species may have come in from the Colorado system. The sucker *Pantosteus jordani* and the dace *Rhinichthys osculus* could have been transferred from the south by capture of headwaters or by alternating discharge of drainage over divides composed of alluvial fans. Some of these transfers may be taking place today, but those known to have taken place in the recent past are confined to headwaters species, and there is no ichthyologic basis for a belief in general drainage of Lake Bonneville to the Colorado. Connections in a northerly direction are more definite, as would be expected from the fact, established on physiographic evidence, that Lake Bonneville discharged to the Snake River and thence to the Columbia. Some of the upper tributaries of the Snake have an essentially Bonneville fauna; for example, *Snyderichthys copei* occurs in the Wood River. The fish data, though inadequately detailed, indicate that most of the upper Snake fauna was destroyed by lava flows, for the endemic genera of the Columbia and the semimarine types (lampreys, sturgeons, salmons) are lacking above the falls. Some of the headwaters escaped destruction, however, and still preserve Columbia, non-Bonneville types (three suckers and a sculpin), while the Lost River group of streams also seems to preserve species belonging to the old Snake rather than the new one (the Dolly Varden, an endemic subspecies of cutthroat trout, and 5 localized endemic races of *Cottus*). The destruction of the fauna antedates the overflow of Lake Bonneville; when the overflow took place some Bonneville types, including one of the endemic genera (*Snyderichthys*), repopulated the streams of the Snake plateau, while by the same route some Columbia types (such as *Richardsonius balteatus hydrophlox*, which occurs above falls elsewhere in the Columbia system) were able to enter Lake Bonneville. The authors believe that at least the endemic *Iotichthys* and the Utah Lake sucker *Chasmistes liorus* existed in the Bonneville basin before the time of discharge, but where these species came from is not clear. That is to say, the mystery of the origin of the peculiar fauna of Lake Bonneville is not cleared up by the discovery of the transitory connection with the Snake. Another mystery is the occurrence of an endemic cisco *Leucichthys gemmifer* (a "subarctic relict") and two other endemic forms of the same family in Bear Lake, which was tributary to Lake Bonneville but outside its highest shore lines.

Lake Lahontan presents a similar problem. Its present remnants, such as Pyramid Lake, contain some highly peculiar types, yet there are obscure suggestions of pluvial connections with adjacent basins and with the ocean. Pleistocene fossils from the beds of Lake Lahontan include a stickleback, *Gasterosteus doryssus*, and a killifish, *Fundulus nevadensis*. These are lowland, coastal and semimarine types, and it is suggested that the Great Basin of Nevada was a coastal lowland as recently as early Pleistocene time. This is perhaps too sweeping an inference,

but it is remarkable that living *Fundulus* and *Gasterosteus* occur in the coastal waters of the Southwest, while two species of *Fundulus* are known as fossils from Death Valley, a third is known from the Mohave Desert (Miller, 1945), and two living genera believed to be derived from *Fundulus* (*Empetrichthys* and *Crenichthys*) are endemic in this region, the first to the Death Valley system and the second to disrupted pluvial tributaries of the Colorado River. All the known early connections of Lake Lahontan, therefore, are to the southwest, and there may well have been an early Pleistocene river system, if not an arm of the sea, in this region, now irretrievably broken up by later Pleistocene orogeny.

There is no evidence, either physiographic or ichthyologic, that Lake Lahontan had an outlet to the sea during the stage of its definitely recorded high-water level. A large number of now-isolated basins to the north, east, south, and west formerly held lakes tributary to the main lake, and some of these still retain a Lahontan fish fauna, while others, particularly to the south, are now fishless. The best indication of a connection with one of the adjacent major basins comes from the Klamath drainage in Oregon, and this indication is very weak. The Klamath system, though it now discharges to the sea, was formerly a basin of interior drainage and has a highly distinctive fauna: 10 endemic species out of 25, and one endemic genus (the sucker *Deltistes*) out of 13. No typically Lahontan species occurs, but the three suckers of the genus *Chasmistes* are most closely related to *C. cujus* of Pyramid Lake and *C. liorus* of Utah Lake (in the Bonneville basin). Even this equivocal evidence of former relationships is weakened by the discovery of fossil *Chasmistes* in the beds of Fort Rock Lake, for this lake may have drained to the Columbia. As the Klamath fauna is composed on the one hand of sharply differentiated endemics and on the other of species either the same as or closely related to widely distributed forms in the Columbia, Sacramento, and other rivers, it is safe to say that if Lake Lahontan discharged this way it must have been a long time ago. The two basins are not now adjacent; between them are several independent basins, which either have no fishes or else have nonindicative species, and also Goose Lake, now tributary to the Sacramento. There is some evidence, however, that Goose Lake and its outlet, Pit River, have been captured from the Klamath by the Sacramento, so that the present geography would not disprove the idea of a Lake Lahontan–Klamath connection if there were stronger supporting evidence.

The classic problem, whether all the lakes of the Lahontan basin dried up during postpluvial desiccation, to form once more after the xerothermic interval or its equivalent, is dismissed by Hubbs and Miller with the statement "we are inclined to favor Hutchinson's (1937) argument" (1948, p. 41). Hutchinson pointed out that the idea that all the lakes of the Lahontan system dried up in postpluvial time is inconsistent with the occurrence of well-marked lacustrine endemics in Pyramid Lake, and argued that Pyramid Lake, at least, must have been kept fresh by overflow. Freshening by desiccation and deflation, however, has probably been a commoner process in the Great Basin. The most interesting new facts bearing on the postpluvial history of Lake Lahontan come from the archaeologic horizon of Lovelock Cave, where samples of the ancient fishes of Humboldt River or Humboldt Lake have been preserved. They include a large sucker, presumably *Chasmistes cujus*, and many lake chubs, among them apparent hybrids between the lacustrine *Siphateles obesus pectinifer* and the fluviatile *S. o. obesus*. This hybridization is going on today, and in fact it is the basis for the removal of *pectinifer* from the genus *Lavinidius*, which Snyder erected for it, and its recognition as a subspecies of *obesus*.

The most satisfactory treatment is that of the Death Valley system, for here the data are most nearly complete, the cyprinodontid fishes in particular having been thoroughly studied by Miller (1946; 1948). Ranking third in area and in faunal diversity among the western basins of interior drainage, this was an integrated hydrographic system during one or more pluvial ages: the Owens, Mohave, and Amargosa Rivers all having drained through a series of large, deep lakes to Lake Manly in Death Valley. That the basin has been isolated for a long time is indicated by the marked differentiation of the fishes; one of the 5 genera (*Empetrichthys*) and 8 of the 10 species are endemic. That there was an "earlier pluvial" connection with the Colo-

rado, however, can scarcely be doubted. The physiographic evidence for this is slight, presumably because subsequent volcanism and erosion have broken the continuity of the old drainage; the most likely route, however, is to the southeast of Death Valley via a series of structural troughs. The ichthyologic evidence consists of the present occurrence of the two cyprinodontid genera, *Cyprinodon* and *Empetrichthys*, and of the fossil occurrence of *Cyprinodon* and *Fundulus*. The only other *Cyprinodon* species known west of the Rio Grande is *C. macularius*, and it is confined to the Colorado. Pleistocene disruption of parts of the old Colorado system has led to the production of two endemic genera of funduline cyprinodontids, *Empetrichthys* with two species and four subspecies in the Death Valley system and *Crenichthys* with two species in pluvial White River and in the Railroad valley. In addition, four species and at least nine subspecies of *Cyprinodon* occur today in fragmented parts of the Death Valley system.

To a certain extent the argument for Colorado derivation of this fauna rests on negative evidence—*i.e.*, the absence of *Cyprinodon* and of derivatives of *Fundulus* elsewhere in the West, and the absence in Death Valley of typical elements of other faunas. It could perhaps be argued that the transfers, though doubtless from the Colorado, were casual, and that the high degree of endemism is due to adaptive radiation in a drainage basin that had some other connection with the ocean or none at all. But two such introductions (*Fundulus* and *Cyprinodon*) are required, and as both point in the same direction the connection seems likely to have been more than casual.

Not all the Death Valley fauna came from the Colorado, for the minnow *Siphateles* (with two species, *mohavensis* in the Mohave River and an unnamed subspecies, apparently of *S. obesus*, in the Owens River) is unknown in the Colorado. These fishes, and probably the Owens River *Catostomus*, which is closely allied to *C. tahoensis* from Lake Tahoe, evidently came in from the Lahontan basin to the north. The evidence of this transfer would probably be stronger if Mono Lake were not without native fishes, recent volcanism in this region having obliterated the faunistic and some of the physiographic evidence for the hydrographic connection. The Owens River *Cyprinodon*, *C. radiosus*, is the most primitive form—*i.e.*, the closest to *C. macularius* of the Colorado. It appears that the drainage of Lake Lahontan to Owens River via Mono Lake could have taken place during the last pluvial age, and that the fish distribution does not imply a connection at the earlier time when Death Valley was acquiring its original fauna from the Colorado. The early discharge of Lake Lahontan to the sea may have been in this direction, as discussed above, but whether it took place through Death Valley or by a more easterly route cannot be settled without more fossil evidence. The beds of all these Pleistocene lakes are probably rich storehouses of fossils, and a huge field of research lies waiting there.

The only remaining fish found in the Death Valley system is the dace *Rhinichthys*, with one form in the Owens River and another in the Amargosa. These are headwaters types, well adapted to dispersal across divides by capture, and there is physiographic evidence of capture of some Las Vegas (Colorado) drainage by tributaries of the Amargosa. Whether the Owens River form came in by the same capture or a different one is problematical; in any case it is most improbable that any cyprinodontids entered Death Valley by such a means.

This discussion may be appropriately concluded with some remarks on the present and on the future state of this kind of research. First, Hubbs and his colleagues deserve the highest praise for the energetic and intelligent way in which they have approached the problem, surely one of the most exciting subjects in all biogeography. Second, we need to know much more of the Pleistocene hydrography and biogeography of Mexico, in order to see how far southward pluvial climates extended and to what extent pluvial ages in the tropics can be correlated with pluvial and glacial ages in higher latitudes. That the Rio Lerma drainage has been disrupted much as has that of the parts of the Great Basin is reasonably clear, but we know virtually nothing of the territory between the Lerma and the Colorado. Even for the Lerma system the information, largely from Meek (1904), is out of date and tantalizing rather than convincing. Finally, these disrupted systems contain many aquatic organisms other

than fishes, but so far they have scarcely been touched.

Chromosome races of Drosophila pseudoobscura.—Nothing better illustrates the scope

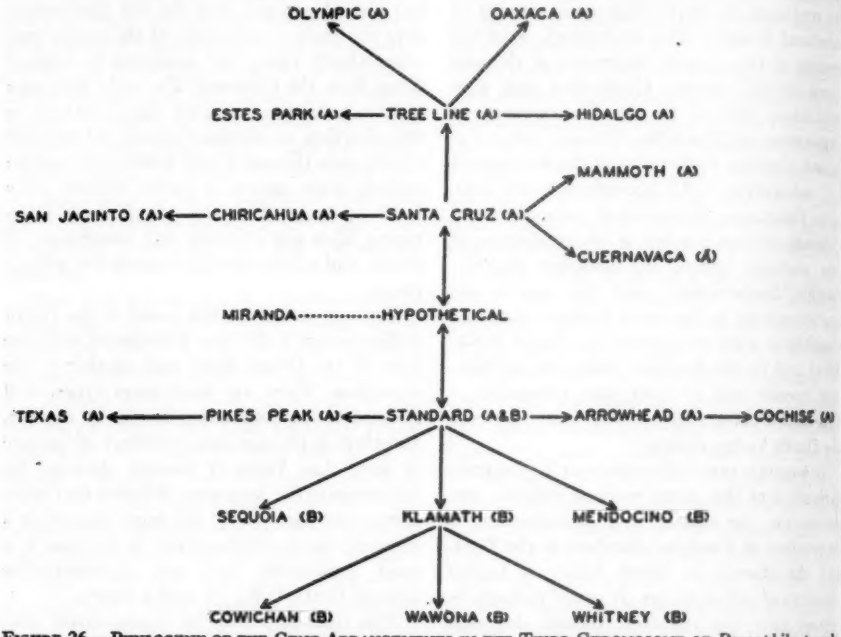


FIGURE 26.—PHYLOGENY OF THE GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura* (A) AND *D. persimilis* (B)
From Dobzhansky (Fig. 5), *in* Dobzhansky and Epling (1944).

and scientific importance of Pleistocene biogeography than the necessity of jumping directly from a consideration of fish distribution to one of *Drosophila* genetics. That the two subjects have anything in common would doubtless have been inconceivable to Mendel, but the fact is that they are intimately related. The important discovery of Dobzhansky and his coworkers, that there are naturally occurring strains of *Drosophila* differing principally in the arrangement of genes along their chromosomes, has been discussed above. It is proper now to give an account of such races of *Drosophila pseudoobscura* (Dobzhansky and Epling, 1944), distinguished on the basis of overlapping inversions in the third chromosome, and of the inferences that seem to follow from a consideration of their geographic distribution. The vitality of this relatively new subject can be judged from the fact that the first discussion by Epling (in Dobzhansky and Epling, 1944) was immediately followed by a symposium (Mayr, 1945; Stebbins, 1945; Simpson, 1945) in which very divergent interpretations of the data were put forward.

The phylogeny of the gene arrangements in *D. pseudoobscura* and *D. persimilis* (formerly called *D. pseudoobscura* race *B*) is shown in Figure 26. One arrangement, Standard, is common to the two species. The assumption that the arrangement called Hypothetical is ancestral fixes the phylogeny, and this is reasonable since the arrangement is closely similar to the one occuring in a third species, *D. miranda*. The common ancestor of the three species may no longer exist, but there are two fundamentally different entities, called *phylads*, within the species *pseudoobscura*, one of which (the Standard phylad) is more closely related to *persimilis* than the other (the Santa Cruz phylad). We are not concerned here with the genetic mechanism by which these arrangements are perpetu-

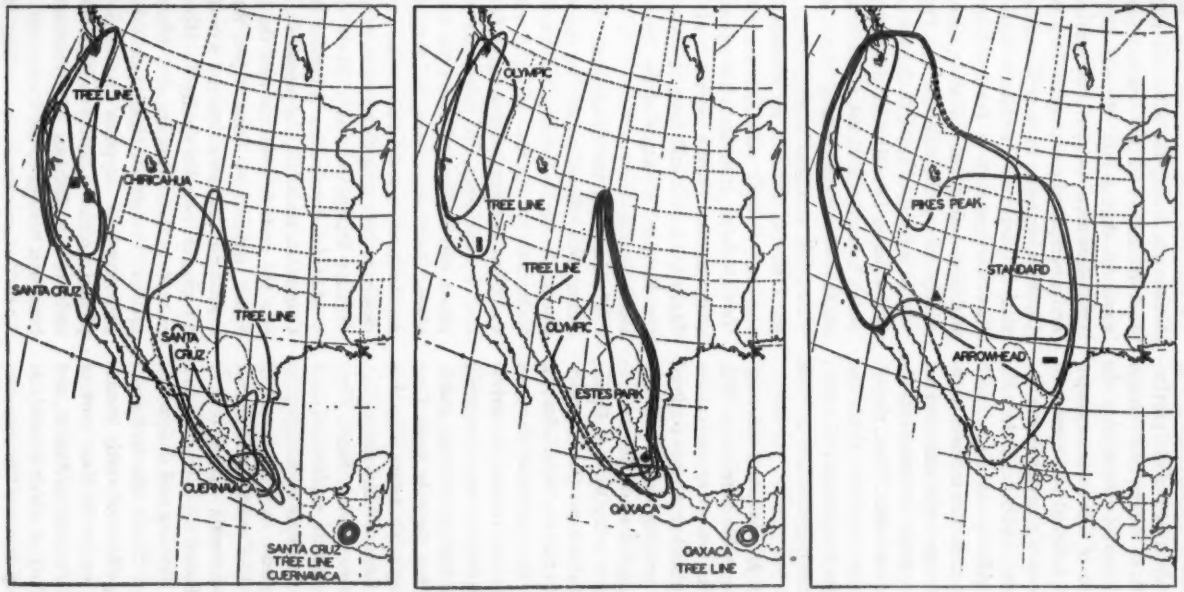


FIGURE 27.—*Drosophila pseudoobscura*

Left, limits of the primary and secondary gene arrangements of the Santa Cruz phylad; center, limits of Tree Line and its derivatives; right, limits of the Standard phylad. The symbols indicate the location of arrangements found in only one or two localities. From Epling (Fig. 1), *in* Dobzhansky and Epling (1944).

ated in the species population; it is sufficient to know that *pseudoobscura* populations are in general discontinuously distributed, particularly in the Great Basin where they occupy montane islands in a sea of desert, that the frequency of occurrence of a given arrangement in a given locality is believed to be constant (with certain exceptions of a cyclic nature discussed by Dobzhansky, 1947), and that the arrangements are evidently associated with gene contents that adapt the flies to the environment in which the arrangements occur and are less well adapted to other environments in which other arrangements occur. Thus, though there is no reproductive isolation within the species, there is geographic isolation of a sort, and at least two species might be said to be *in statu nascendi*.

The two phylads of *pseudoobscura* differ significantly in their geographic distribution (Fig. 27). Standard and its secondary derivatives Pikes Peak and Arrowhead are largely confined to the United States, avoiding southern Mexico altogether, and the phylad seems to center in the Great Basin. This is taken by both Epling and Mayr to mean that it arose (*i.e.*, is associated with gene contents that are better adapted) in a drier climate than that characterized by the Santa Cruz phylad. Santa Cruz and its derivatives have a strikingly disjunct range, centering in the coast ranges, in highland Mexico, and in highland Guatemala, but the only Santa Cruz arrangement occurring with appreciable frequency in the Great Basin is Chiricahua.

The disjunct pattern of the Santa Cruz phylad certainly requires an explanation, and the most reasonable hypothesis would appear to be one involving spread from the western United States along the Cordilleran highlands into Mexico and Guatemala during one or more pluvial ages, followed by disjunction as a result of postpluvial warming and desiccation. Epling, however, in a closely reasoned argument, supports a hypothesis of vastly greater age. Leaning heavily on the brilliant work of the paleobotanists Chaney, Berry, Axelrod, and others (a fuller summary of which is available in Cain, 1944a), Epling discusses the migration and restriction of two major forest types from the Eocene to the present. On the one hand the Arcto-Tertiary forest, a moist, warm-temperate type, holarctic in distribution during the Eocene, expanded southward to Mexico and Guatemala during the Miocene. With cooling and desiccation of the western part of the continent during late Miocene and Pliocene time, elements of this forest became ecologically and geographically segregated from each other. On the other hand, more xeric types of vegetation, in particular the Madro-Tertiary forest that was centered in the northern Mexican highland before the Miocene, spread more widely during the Miocene and Pliocene. In part as a result of uplift of the western United States during late Miocene and early Pliocene, which brought the Great Basin into the rain shadow of coastal ranges, elements of this sclerophyll woodland reached as far north as the Columbia Plateau. By subsequent restriction and ecologic differentiation the Madro-Tertiary forest or savanna has retreated to the southwestern United States and northern Mexico, where it still forms a wedge between the disrupted remnants of the Arcto-Tertiary forest.

The fact that the chromosome races of the Santa Cruz phylad avoid the region that is essentially Madro-Tertiary in climate and vegetation and are disjunct with the remnants of the Arcto-Tertiary forest seems to Epling more than a coincidence. He points out that many genera and families and even a few species show almost identical patterns, and that *Drosophila pseudoobscura* resembles these plants even more closely in belonging to a species group with a disjunct European-western North American-Guatemalan distribution. A familiar example is *Chimaphila umbellata*, the pipsissewa. He notes also the geologic evidence that the low-lying, humid Isthmus of Tehuantepec, where *Drosophila pseudoobscura* does not now occur, was a region of low relief during the Miocene, submerged in late Miocene and Pliocene, and uplifted (though not higher than today) in the Pleistocene. He supposes that the Santa Cruz phylad, because it occurs on highlands at both ends of the Isthmus of Tehuantepec, and because it belongs to the Eocene and Oligocene Arcto-Tertiary forest, is at least as old as Miocene. (On this hypothesis the secondary inversion Tree Line and the tertiary inversion Olympic must also be as old as the Arcto-

Tertiary forest, while Oaxaca, another tertiary inversion, must antedate the submergence of the Isthmus of Tehuantepec.) In support of this breath-taking concept Epling cites evidence that evolution in insects has virtually ceased since the Oligocene. (Stebbins goes further and maintains, erroneously according to Simpson, that the genus *Drosophila* occurs in the Baltic amber.) He also reviews the available data on Pleistocene climates and concludes that outside the glaciated regions conditions during the Pleistocene were so little different from today that one *must* go farther back in time to find adequate causes for the spread and the later disjunction of the Santa Cruz phylad.

Mayr, who initiated the symposium on Epling's theory, was not slow to challenge the high antiquity postulated for the present range of an existing species. In effect, he took his customary position, derived fundamentally from the study of island faunas, that the powers of dispersal of organisms have been enormously underrated by biogeographers, and that even Pleistocene relicts are improbable among winged forms. Mayr has few equals in a polemic of this sort, and he made the characteristic remark that "the gap between the Mexican and the Californian ranges of Santa Cruz could easily be bridged by a ten-hour drift of a gravid female during a heavy storm" (1945, p. 77). In taking this position Mayr has undoubtedly gone too far; heavy storms and other modern methods of dispersal are scarcely likely to have carried all the disjunct plants at the same time, and the problem of relicts cannot be so lightly dismissed.

The arguments of Stebbins and Simpson largely cancel each other out, for they deal with the probability that evolution of some species of *Drosophila* is as slow as Epling's hypothesis requires. More to the point is the question, whether the distribution of a species can be so old, and in this connection it is rather distressing to find the "new systematics" so heavily contaminated by the "old biogeography," as shown by the tacit assumption of Epling and Stebbins that the age of the species and the age of its distribution pattern are identical.

In view of the fact, made abundantly clear in the last section, that Pleistocene climatic changes in the Great Basin and farther south were extensive and of a sort making it possible for northern species to penetrate into the subtropical zone of high atmospheric pressures, there would seem to be a prior probability that the geographic disjunction of the Santa Cruz phylad, at least, is of Pleistocene origin. It is important, therefore, to inquire into Epling's reasons for denying this probability. These are, first, Meinzer's opinion that really moist pluvial climates were confined to higher latitudes, and that conditions in the southern part of the Great Basin were less strikingly different from today; and second, the fact that Pleistocene floras from California indicate climates that differed little, if at all, from those of the present.

Both these lines of evidence, however, are based on inadequate information. As Meinzer's conclusion depends on the absence of Pleistocene lake deposits and shore lines in closed basins in southeastern California and trans-Pecos Texas, it is useful to remember (1) that closed basins are less well developed there than in Nevada and Oregon, (2) that trans-Pecos Texas in particular has been very little explored, (3) that evidence of Pleistocene lakes is not always so easy to find as in the basin of Lake Bonneville, (4) that the Valley of Mexico held a large pluvial lake, which on ichthyologic evidence may have drained to the Rio Lerma, and (5) that the rest of the plateau of Mexico, the basin of the Laguna de Mayran for instance, has never been carefully searched by a Pleistocene geologist. Our knowledge of the Pleistocene of California is just as deficient: four important fossil beds are known, from Santa Cruz Island, Rancho La Brea, Carpinteria, and McKittrick, and while it may be true that their fauna and flora imply climatic conditions not very different from today (Miller, 1940), there is nothing to show that all of these deposits are not interglacial in age. The numerous fossil birds from deposits of pluvial lakes, Fossil Lake, Oregon, for example (Howard, 1946), though interesting, do not help very much, as they were mostly water birds of the same species (with the exception of the flamingo) still found around lakes in the region at present. The demonstration by Stearns (1942), on the basis of the fossil occurrences of the marmot *Marmota flaviventris obscura*, that the life zones of New Mexico must have been shifted downward by some 4000 feet

during a Wisconsin subage, gains new significance in the light of this controversy. But on the whole we know little that is relevant about the Pleistocene of western North America, and Epling is mistaken in thinking that we do.

Summary and Conclusions: Europe and North America

Outline

From the standpoint of Pleistocene biogeography North America and Europe resemble each other closely, and differ in the character of their problems rather sharply from Africa, southeastern Asia, and South America. As would be expected, the two continents where continental glaciation occurred on the most extensive scale differ from the rest of the world where glaciation was confined to high mountains, and where the more spectacular climatic changes during the Pleistocene were in the direction of increased precipitation rather than refrigeration. For this reason some stock-taking can be done appropriately at this point in the review.

Because the attempt has never been made before, and therefore seemed eminently worth making, there has been an effort in this presentation to look at existing animal and plant distribution as a whole from the standpoint of Pleistocene geography. The volume of data is so stupendous that complete treatment is obviously impossible, but the material included is believed to be fairly representative. What does it all add up to? Is biogeography of interest solely to biologists, or is there anything in it that geologists and other Earth scientists can use? Without anticipating the data from Africa and elsewhere, we shall give a preliminary answer to this question, first, by showing that many biogeographic facts are extremely limited in their application or perhaps useless, and second, by pointing to instances in which the biogeographer can help to solve problems not otherwise susceptible to attack.

Limitations of Biogeography

The nunatak hypothesis of Fernald, which has its counterpart in western Europe, is an example of a biogeographic argument that is almost or entirely useless to the geologist. This argument starts with the occurrence in some locality of species of plants or animals (usually plants) that are widely separated from their nearest relatives, either of the same or of related species, and that seem, by reason of their apparent inability to spread or of their endemism, to have been isolated in their present situations for a long time. Some of the areas in which they occur are famous among geologists for the paucity of convincing evidence of overriding by an ice sheet. Later geologic work in the same areas has sometimes produced such evidence; probably other areas really were nunataks throughout a glacial age as they certainly were during early phases of deglaciation. Backed by geologic authority, the biogeographers have not hesitated to maintain the existence of a correlation between supposed nunataks and the stations of the remarkable relict species, and have accordingly supported the idea of survival of the plants in their present habitats through a glacial age.

For some species, such as those that now occur in Greenland and particularly those that have been found growing on nunataks, this hypothesis is certainly correct. If there were nunataks projecting above the continental ice sheets, species are known that could have survived on them. Many of the plants for which glacial survival is postulated, however, are decidedly not of this character (orchids, for example), and it is evident that there must be something wrong with the hypothesis. When it is realized that many relicts of the same sort occur in places known to have been covered by ice and later to have been submerged under late-glacial seas, it is obvious that distribution pattern in itself is insufficient proof of survival through a glacial age. That is, there is a biogeographic weakness in the argument, and some of the most narrowly localized endemics and the most spectacular disjuncts must have been migrating more in postglacial time than could be admitted by the proponents of the nunatak hypothesis.

The same sort of weakness is inherent in other theories of glacial survival. In the foothills of the Alps, for example, isolated remnants of erosion surfaces now shelter narrowly localized endemics and peculiarly disjunct organisms

(beetles in particular having attracted attention among animals, doubtless because their distribution is better known than that of most animal groups). These remnants, known as *massifs de refuge*, are supposed not to have been glaciated during the last (Würm) glacial age, though they may have been so during Mindel or Riss ages. It is difficult to disprove the notion that the beetles survived the Würm glaciation in their present habitats, but, as many other lines of evidence indicate that relict species have not always lived in what are admittedly relict habitats, but have reached them in postglacial time, the suggestion should not be accepted uncritically. Probably it is admissible for some species.

Glacial survival has been passionately urged for components of the fauna and flora of the British Isles, especially Ireland. Here a new feature is brought into the debate, namely the existence of land bridges. Ireland is believed on geologic grounds not to have been joined directly to England since the climax of the last glacial age, or since a time when only arctic species could have made the crossing by land. By the Boreal phase of postglacial time, when the climate had so far ameliorated as to permit immigration of temperate species, the Irish Sea was certainly in existence. The geologic facts agree with, and are even confirmed by, the distribution of the smaller land mammals of the British Isles, for Ireland lacks many of the species that might be expected to live there, such as the mole, the common shrew, and all microtine rodents. Of the several waves of migration of mammals into the British Isles that can be discerned in the purely zoogeographic data, only the first has reached Ireland which therefore must have been cut off rather early from free access by land. On the other hand, the presence in Ireland of disjuncts of "Lusitanian" distribution that seem to have required a land bridge to get there poses a serious dilemma. Lusitanian species are southern types that evidently require warm winters; their occurrence in England is irrelevant, for they could have been, and probably were, isolated there by climatic changes subsequent to the climatic optimum, but if they reached Ireland by a land birdge they must have survived the last ("New Drift") glaciation in Ireland. This seems highly unlikely in view of their ecologic character, but the Irish case is the strongest one yet made out for survival through a glacial age.

Land bridges constructed on biogeographic evidence alone are notoriously flimsy. The modern biogeographer regards the best of them with scepticism. Mayr, in his consideration of the fauna of islands, has been one of the leaders of the new school, which maintains that the powers of dispersal of organisms have been vastly underrated in the past, and that given suitable habitats and a sufficiently long time for dispersal there are no barriers to colonization that cannot be surmounted by some animals and plants. Mayr has occasionally gone too far in arguing for this position; but it is surely fair (if somewhat guarded) to say that almost any given species can get to almost any suitable habitat by crossing any geographic barrier, and that an island, for example, must contain a whole balanced segment of a continental fauna before a land bridge has to be postulated. That there were land bridges from France to England, from China to Japan, and from Malaya to Java and Sumatra, cannot be denied, but in these cases the proof is not entirely biogeographic. In the Irish example, where the existence of a land bridge is not in doubt, but where the question of its age is of crucial importance, we are entitled to look with suspicion on the idea of a land connection before the last glacial age, for the list of Lusitanian species that seem to require such a connection is small.

There is another sphere in which the weakness of biogeography is apparent. In the southeastern United States, for example, the occurrence of many species and genera, believed to be old partly because of fossil evidence and partly because they are widely isolated from their closest relatives in eastern Asia, has been misinterpreted. This celebrated problem is not customarily regarded as a Pleistocene matter, but it has an important bearing on the Pleistocene nevertheless. If the species have been in their present habitats (old land areas, preglacial river systems, peneplane remnants, and the like) since early or middle Cenozoic time, it is difficult to understand the obvious fact that Pleistocene climatic changes in the general region were extensive. That is, the evidence

from Pleistocene fossils (walrus in South Carolina, white spruce in Louisiana, etc.) conflicts with the pattern of existing distribution as interpreted by biogeographers. Though many aspects of this question have been left open, an attempt has been made to clear away some of the conflict and some of the misconception by pointing out that, while southeastern North America taken as a whole may have served as a refuge for temperate and boreal species, the old species have not necessarily persisted in their present localities throughout the Pleistocene. Like the narrowly localized relicts, to explain which the nunatak hypothesis was erected, the relicts on peneplane remnants must have been moving around during glacial ages, some of them perhaps having been driven into Mexico and peninsular Florida. To put it in another way, as in the case of the organisms allegedly unable to cross a water barrier, their powers of postglacial and present-day dispersal have been underestimated.

It is especially discouraging to have to report that biogeographic data fall short of proof even where there are strong *a priori* grounds for adopting a suggestion. This is the case with the hypothesis that multiple glaciation is reflected in the existing distribution of species, in the Alps or in northern Europe, for example. There are indications everywhere that the biota is not all of one age. Sometimes close study of a genus shows ancestral, derived, and obviously new species all occurring in the same general region; sometimes, because the coexistence of sibling species implies differentiation in previous isolation, several kinds or stages of isolation can be discerned in the makeup of a single animal or plant community, and glaciation is the most probable cause of such isolation. Probably the strongest case for multiple glaciation can be made of the existence of boreo-British and boreo-alpine distribution patterns, the argument being that if it took one glaciation to produce the boreo-British arrangement (Scandinavia and the British Isles), *à la* Darwin, it must have taken two glaciations to produce so striking a configuration as the boreo-alpine. This view finds support in the frequency of taxonomic divergence among boreo-alpine species, for in many instances it happens that one subspecies is boreal, the other alpine. But all such arguments assume evolutionary rates to be essentially uniform among organisms, and are therefore untenable, despite the inherent reasonableness conferred on them by the existence of multiple glaciation as an established fact.

The case against biogeography, then, might be summed up as follows: for certain types of problem, including survival of species through a glacial age, and the construction of land bridges on the basis of the distribution of individual species that seem unable to cross a water barrier, biogeographic data are inadequate and may only confuse and irritate the geologist. The distribution of every species is virtually a law unto itself; worse, it is a law that is incapable of precise formulation, and that nobody understands fully, for every change of range may have a separate explanation. There are relict species, and there are relict habitats, but the present occurrence of the species in the habitats is no proof that they have always been there. The occurrence of a genuine fossil in a particular locality and in a particular stratigraphic context, of course, is a different kind of biogeographic datum altogether; this sort of evidence of Pleistocene geographic conditions is not being criticized, and one only wishes there were more of it. But the existing distribution of animals and plants is subject to such discordant interpretation that the geologist cannot be blamed for despising it.

Value of Biogeography

There would be little point in continuing with this review, or in publishing what has already been written at such length, if the above were the only conclusion to be drawn. Fortunately, it is not. There are circumstances in which biogeographic data are not only worthwhile but indispensable. This seems to be the case with at least two major types of problem; (1) former land connections, and (2) former stream connections. In summarizing the contributions of biogeography to each of these in turn, we shall have to be careful to distinguish the validity of the data themselves from the validity of the interpretations that have often been placed on the data. This is absolutely necessary, because, of all the lines of scientific reasoning with which the writer is acquainted, that of biogeography is the most thickly beset by pitfalls. Some of

these have already been hinted at in the preceding section, and it would be rash indeed to pretend that they have all been avoided in this review.

In the preceding discussion of land connections between islands and continents, criticism was explicitly directed to "the construction of land bridges on the basis of the distribution of individual species that seem unable to cross a water barrier." When balanced segments of continental faunas are found on islands, however, the case for a former land connection gains enormously in respectability. By "balanced" it is understood that the total number of terrestrial species on the island is about the same as on a portion of the continent of equal area and ecologic diversity, and that the island shows the appropriate proportions of carnivores and herbivores among animals, lower and higher types among plants, and narrowly and widely distributed species among both plants and animals. What constitutes balance in any specific example, or how great a degree of imbalance is to be expected in the biota of a continental island, will always be matters for debate among biologists, for when islands are separated from continents evolutionary divergence proceeds apace. Thus the organisms of long-separated islands may differ more from those of an adjacent mainland than do those of two separate continents, as the example of Madagascar shows. The point is none the less clear, that most of the older land bridges, constructed by biogeographers specifically to account for the distribution of particular species (more often genera or families), are invalid.

Used with intelligent awareness of past blunders and the reasons for them, biogeographic data are still of the utmost value in the study of former land connections. Their value arises from the fact that orthodox geologic data are obtainable with difficulty or not at all in this type of geographic problem, the region in which direct evidence is to be sought being under water and the evidence itself often having been removed by subaqueous erosion. Various indirect procedures have then to be resorted to, of which biogeographic research is not the least important.

The British Isles provide the classic example. Land connections between Great Britain and Europe have existed at various times in the Pleistocene. Exactly when they existed and how long they lasted is not definitely known; there are many obstacles to detailed correlation between British and continental Pleistocene stratigraphic sections, and this is an important subject for future research. For postglacial time, however, the picture is gradually becoming clear. To a considerable extent our knowledge is the outcome of more or less orthodox geologic methods: the fact that peat occurs *in situ* on the Dogger Bank has been of enormous help, and other stratigraphic evidence is still accessible by boring in coastal deposits. But the preservation of so much of this kind of evidence is a piece of extraordinary good fortune, not to be counted on elsewhere. Even the Irish geologists have not been so lucky, for the floor of the Irish Sea seems to have been considerably remodelled since its submergence. In this situation it is of concrete help to know that the Irish fauna and flora are balanced (proving that land connection once existed between Ireland and Great Britain), but show striking lacunae (of such a character as to show relatively early severance of the connection). Other biogeographic data are of equal importance in filling in local details. For example, the Isle of Man was evidently separated from England before England was separated from the Continent, and Guernsey seems to have been separated from France before England was, while the absence from the British Isles of a number of beetles belonging to beech forests implies that the formation of the English Channel antedated the spread of the beech. Some of these facts are of course known from other kinds of evidence, but it is worth reiterating that we cannot always expect to find such evidence, and may be forced to depend on biogeographic data for a solution to the problem of former land connections.

The problem of Corsica is discussed as an example where stratigraphic information is lacking, at least up to the present, but where the distribution of the land mammals is of definite value in indicating recent land connection, in this case with Italy. Some more spectacular instances will be discussed in the chapters on Africa and eastern Asia. North America, so far as the writer is aware, provides no comparable case, and the realization that this is so focuses attention on the island of Newfoundland. Ma-

terial probably exists in the literature of special groups, such as mammals, for an interesting investigation of this island, but so far no one appears to have tried to see what bearing it may have on glacial and postglacial changes of land and sea in eastern North America.

In the second type of problem, that of former stream connections, North American work has been of exceptional utility and interest. Here again two points require emphasis. The first is that the facts must be used intelligently. Direct connections by water between now-separated stream systems, when postulated on the basis of the distribution of particular species, are no more likely to withstand critical attack than are the older land bridges. Whole, *i.e.* balanced, segments of the biota must be found to be transferred before it is safe to conclude that a former connection has existed. The second point is that the service of the biogeographic information consists of its uniqueness: deposits laid down by former streams, particularly the late-glacial streams that carried meltwater across now-existing divides, are notably unfossiliferous; much of this material has been removed from the scene by later erosion, and for various other reasons this problem resembles the preceding one in that stratigraphic facts are difficult to get. The worth of the biogeographic observations is thereby automatically enhanced.

The former stream connections that have been most extensively investigated by biogeographic means are those related to the late-glacial drainage of the Great Lakes. Though the lakes all drain to the St. Lawrence River at present, the great bulk of their aquatic biota has immigrated from the Mississippi system. All the known major discharge channels have been utilized in this invasion, and many minor and local peculiarities have turned up in the distribution of individual species of fishes and mollusks. Only a few of these have been cited in the text; emphasis has been placed on cases where the biogeographer has been of material aid to the geologist in pointing to unsuspected connections of drainage. Some of these instances may be found not to meet the rigid requirements previously set up for the acceptance of biogeographic testimony. Taken all together, however, they carry a larger implication: so many (that is, so large a proportion) of the fishes of Wisconsin (for example) have evidently used glacial connectives, that these waters must have been warmer than one might have supposed.

The most dramatic example of the use of fish distribution for the tracing of Pleistocene drainage systems comes from the Great Basin, where Hubbs and Miller have been working with great energy and skill. Many problems remain: we still do not know where the peculiar fauna of Lake Bonneville originally came from, and Lake Lahontan also remains as isolated as ever, despite vague indications of a former continuity with the Klamath system or with the Colorado basin. But in many now-independent basins of this formerly well watered country the ichthyologic and the physiographic evidence of pluvial connection are in splendid agreement, and there can be little doubt that the Death Valley system received its small stock of fishes from the Colorado.

It is not yet clear how far south pluvial conditions extended during the Pleistocene, for this subject has been little studied in Mexico. The importance of filling this gap is heavily underscored; not only is it vital to the biologist to know whether a desert barrier in this region has always opposed southward migration of northern species with the same success as today, but the basis of the correlation between glacial ages in high latitudes and pluvial ages in the tropics ultimately depends on the answer to this question. At any rate, the configuration of the New World seems to be more favorable for an attack on this celebrated issue than is that of the Old World, where a water barrier (the Mediterranean) hinders the application of biogeographic data to the solution.

Certain matter to be found in the paper is not summarized here: in particular considerable portions of the text are devoted to a review of the Pleistocene stratigraphy. With the exception of the treatment of the postglacial stratigraphy of eastern North America, which is epitomized in Table 7, however, none of this is original or new. It may be permissible to paraphrase D'Arcy Thompson, who said of his book *On growth and form*, that it needed no preface, for "it is all preface"; these sections are "all summary".

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

4. PLEISTOCENE VERTEBRATE PALEONTOLOGY IN NORTH AMERICA

By Claude W. Hibbard

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Introduction

Pleistocene vertebrate fossils are found in every North American museum that possesses a collection of fossil vertebrate remains. Many specimens were collected when attention was centered on remains of greater antiquity. Although much of this material has been stored without adequate documentation (according to present-day standards), many scores of species of Pleistocene vertebrates have been described from it.

Most of this material originated in nonglaciated areas, and geologists have overlooked a majority of the fossiliferous deposits. Most of the fossil-bearing Pleistocene deposits of continental origin are scattered, or exist only as stream terraces in noncontinuous deposition, and have not been studied extensively by stratigraphers. Most of these deposits contain many invertebrates, whose remains have not attracted the invertebrate paleontologist since a thorough knowledge of the recent mollusks would be required before the late Cenozoic remains could be interpreted. On the other hand, students of conchology have been too absorbed in a study of living animals to review and interpret the Pleistocene forms. The vertebrate paleontologist has by-passed the fertile field of Pleistocene microfaunas in favor of the larger and more spectacular remains. The neozoologist, through the lack of geologic and paleontologic backgrounds, has overlooked the aspects of Pleistocene animals in the late Cenozoic deposits and has been concerned with the Recent horizontal functions of speciation and distribution of living animals, while only speculating on the phylogeny of their ancestors.

When continental glaciation was first recognized, a change in climatic conditions and faunas was postulated for the regions affected by the ice. Scott (1898, p. 537–538) and Chamberlin and Salisbury (1909, p. 914–917) discussed the probability of successive shifts of Pleistocene faunas and floras. Coleman (1894, 1901) was the pioneer in America who attempted to work out a succession of glacial and interglacial

floras and faunas. This early work definitely demonstrated a succession of shifting floras in North America.

Many attempts have been made to develop a succession of Pleistocene vertebrate faunas in North America to correlate with the glacial and interglacial ages. Those interested in the history of these attempts are referred to the following papers: Cope, 1895; Osborn, 1910; Hay, 1912; 1923; 1924; 1925a; 1925b; 1926; 1927; Baker, 1920; Romer, 1933; Lugn and Schultz, 1934; Schultz, *in* Lugn, 1935; Barbour and Schultz, 1937; Schultz, *in* Condra, Reed, and Gordon, 1947; and Colbert, 1937.

In these studies are listed many forms occurring in the Pleistocene deposits of North America. Some of the workers have grouped the Pleistocene mammals into glacial and interglacial ages, while others have grouped the forms only as early, middle, or late Pleistocene forms. The groupings have been open to question owing to the unknown vertical distribution of the forms. Where attempts have been made to correlate vertebrate forms with glacial and interglacial ages, the jump correlations from nonglaciated to glaciated areas have been open to question, since direct interfingering of the deposits could not be demonstrated. Futhermore, no vertebrate fauna is known from glacial or interglacial deposits of the glaciated region of North America. Such a fauna would give an index for correlation with known faunas from nonglaciated areas.

No correlation of a Pleistocene vertebrate fauna with a glacial or interglacial age can be made until deposits in nonglaciated areas containing the vertebrate and invertebrate remains are carefully studied and correlated with glacial and interglacial deposits.

Good summaries of the Pleistocene fossil record in North America are given by Romer (1945, p. 568–572) and by Flint (1947, p. 521–535).

Pleistocene Faunas

The Pleistocene epoch was so short as compared with the other epochs of the Cenozoic that, had it not been for glaciation, the Pleistocene could not be separated from the Pliocene epoch. However, because of the development of distinct and sharply marked Tropical, Temperate, and Arctic zones during glaciation, part of the Pleistocene can be differentiated rather distinctly from the Pliocene.

In North America nothing is known of the forms which lived in mountainous regions, exclusive of the intermontane basins, or in the polar region throughout the Cenozoic when there was a rather mild climate in those areas. With progressive cooling, which began early in the Cenozoic, these regions became the first potential areas for the development of plants and animals with tolerance for the more extreme cold which was to come later. It was not until late in the Pleistocene that such specialized forms as the woolly mammoth, woolly rhinoceros, and musk-ox became "chained" to the tundra regions. A number of forms which lived in rather mild temperate conditions during the latter part of the Cenozoic became adapted, by the close of the Pleistocene, to the cool conditions to which they were subjected during glaciation. An example of this is the genus *Mammut* to which the American mastodon belongs. The subgenus (*Miomastodon*) of the genus *Mammut* arrived in North America during very late Miocene or early Pliocene time. The beginning of the Pleistocene would not be postulated as coincident with the appearance of the genus *Mammut*. No genus of mammal is known whose first appearance can be used as a sure marker for the beginning of the Pleistocene in North America. The Pleistocene should be limited to the time of glaciation, based upon geologic evidence of ice or upon evidence of faunal or floral changes caused by cold conditions in the Holarctic region. Geologically speaking we are still in the Pleistocene. To draw a line between the Pleistocene and Recent is pure arbitration. It is here recommended that the proposal of Flint (1947, p. 209) that, "the term *recent* be used only in an informal sense", be accepted. In nonglaciated regions of North America it is impossible to distinguish a Wisconsin glacial fauna (a fauna that occupied that region at the maximal extent of the ice sheet) from a postglacial fauna (a fauna that occupied the area after the ice sheet began to recede). Faunas lag in their retreat, and most, if not all, of the retreat of forms in the southern limits of their range, after the ice begins to recede, is by death of individuals. The faunal shift is by population spread, not by migration of the southern individuals. A Pleistocene fauna

that lived in a tundra region or at the edge of a continental glacier, at the time of the glacier's most southern advance, was a glacial fauna at that time. This fauna receded with the glacier and became in part, or wholly, the tundra fauna of the Arctic region of the following interglacial time. The other forms of animal and plant life living at the time of the maximal glacial advance, along the borders of the tundra region or in the tropics, constituted the glacial fauna and flora of their respective regions. With the recession of the ice the same forms except for those exterminated, shifted their ranges wholly or in part, or remained nearly stationary. They became the interglacial fauna or faunules to which new elements from other regions might be added.

A major retreat of the Wisconsin ice occurred before the Wisconsin fauna of North America in the northern part of the Temperate zone changed appreciably. The faunal change came with the extinction of the elephants, American mastodon, camels, the peccary (*Platygonus*), *Cervalces*, *Bison antiquus*, the northern Pleistocene bison (*Bison occidentalis*), the woodland musk-ox (*Symbos*), the giant beaver (*Castoroides*), and other genera. These vertebrate groups became extinct some time after the last ice sheet began to shrink. Evidence suggests that some forms died out less than 8000 years ago.

When compared with the past, the conditions at the present time correspond to those in the first part of an interglacial age. Records show that we have not reached the optimum of earlier interglacial ages. Geologically speaking, the present is a time of glacial recession, though much of the continent was never covered with the Wisconsin ice sheet. Some plants and animals have followed the retreat of the ice sheet and are now living in areas once covered by the ice; their occurrence in these areas is known as post-Wisconsin in relation to the ice sheet proper. Paleontologically speaking we are in a post-American-Mastodon faunal age.

The first glacial fauna of the North American continent to inhabit the nonglaciated regions in front of the ice was chiefly descended from hardier Pliocene forms that had inhabited the polar and high-mountain regions of North America, and included forms already in the area, that certainly possessed wide tolerance and were able to adjust to the changing climate. There was no great change between the last Pliocene fauna and the first Pleistocene fauna. The elements of the two faunas were the same, except that those forms with limited tolerance for the increasing cold were exterminated or forced to shift their ranges farther southward. The great change between Pliocene and Pleistocene faunas did not occur with the first advance of the ice but after the speciation and extinction of numerous late Pliocene forms along with the introduction onto this continent of elephants, bison, and other Asiatic forms. The first glacial fauna of the tundra region in front of the ice would be expected to be the smallest of the Pleistocene faunas, since that fauna would have been subjected to the first severe "weeding out" of forms not adapted to such climatic extremes. Floras and faunas lag in their adaptations to climatic changes.

If it could be fully realized that the climatic conditions which exist at the present time in the temperate and polar regions are the exception in geologic history, and that these conditions have not always existed in the past, a better understanding of the Pleistocene would be gained.

The rate of advance and retreat of the ice was about equal to the pace of plants and snails which moved in front of the glacier both in advance and retreat. Such slow movements of faunas and floras are not migrations in the sense of movement of individuals.

The statement of Meade (1945, p. 519) that "...it is doubtful whether Nebraskan and Aftonian faunas can be differentiated", is not acceptable since optimum glacial and optimum interglacial faunas can be differentiated in North America. However, the study of Pleistocene faunas in North America has not progressed to the point at which a conclusive discussion of the faunas can be attempted as Zeuner (1945) has attempted on the European Pleistocene faunas. There is evidence of Pleistocene faunal shifting in North America.

Pleistocene Faunal Studies

Most of the papers on Pleistocene vertebrates have described new forms or the occurrence of isolated finds.

Cope, Brown, Gidley, Hay, Matthew, and J. C. Merriam and his coworkers contributed

chiefly to our early knowledge of local Pleistocene faunas. Later studies of local faunas are very numerous. Stock and his students, especially, have made outstanding contributions to our knowledge of vertebrate faunas. The contribution of Hubbs and his students, especially that of R. R. Miller (1946) and Hubbs and Miller (1948), both to Recent and Pleistocene ichthyology and Pleistocene hydrography, should not be overlooked.

Few students have attempted to make order out of the chaos that exists in many of the Pleistocene genera. Special attention should be called to the work of Simpson (1941; 1945), on the large Pleistocene cats and on the Pleistocene tapirs, and to the work of Skinner and Kaisen (1947) on the revision of the genus *Bison*.

One of the common errors in the study of fossils is the failure to consider as a unit the assemblage from a given horizon. It is the overall picture of a fauna and the conditions under which these forms were preserved that reveals the paleoecology. The abundance or scarcity of forms in a fauna frequently gives a clue to past conditions. (*See* Stearns, 1942.) Too many papers only describe a new form and do not evaluate the position of that animal in relation to other animals other than taxonomically. As far as the descriptive work is concerned, the form lived entirely by itself, and its place in the stratigraphic column is only approximate.

Paleontologic work has progressed so that very accurate taxonomic, morphological, stratigraphical, and environmental studies can be made of any deposit and the contained fossils by specialists. The great scarcity of specialists in the fields of Pleistocene Paleo-ornithology, -herpetology, and -ichthyology will be felt for some time in the complete evaluation of Pleistocene faunal studies.

Paleontologic interpretations of past conditions are based chiefly upon the knowledge of present animals, and of their ecology. It is assumed that by the time the genus *Notiosorex*, the genus *Sigmodon*, the subgenus *Mictomys*, the Operarius group of *Microtus*, etc., appeared they possessed chiefly the habitat preferences of their living representatives. If such assumptions are not possible, it will never be possible to unravel Pleistocene history. Any study of past faunas is at best open to question. It is necessary to realize the limits in such work and proceed with the greatest caution and accuracy. Simpson (1936) has fully discussed the relationships of local and continental mammalian faunas, and workers interested in the correlation of local faunas should study this paper.

In the past the great stumbling block to a study of paleoecology has been the neglect of the associated smaller members of a given fauna. A few of the large forms may be used as indices for environmental conditions, but most of the larger mammals possess a wider range of tolerance than do smaller forms. For example, at the time of the settlement of America, the cougar (*Felis concolor*) ranged from the Atlantic Ocean to the Pacific Ocean and from British Columbia to Patagonia. Remains of this cat in Pleistocene deposits confirm its past distribution, contribute to its known vertical range, and are useful as a basis for assuming the presence of certain animals used as food. On the other hand the finding of the remains of the lemming, *Synaptomys* (*Mictomys*) *borealis*, in Pleistocene deposits indicates that at the time the deposits were laid down ecological conditions in the area were similar to the ecological conditions under which we find the lemming living at the present in the Boreal region.

In general, the smaller forms have rather restricted habitats and are the best indices for the study of past climatic conditions. It also appears that among the smaller forms there is the greatest amount of extinction and probably of speciation, which makes small mammals the best horizon markers known for a stratigraphic study of the Pleistocene. This makes the paleontologist's problem more difficult, for he must know the living forms in the groups with which he works.

Shifting of Pleistocene Faunas

General Discussion

During the past 10 years considerable progress has been made in the study of Pleistocene vertebrates in North America, owing to improved methods of collecting, more detailed studies of Pleistocene stratigraphy, and efforts to collect all remains of animal life from a particular zone.

There is a difference between an exposure

containing fossils and a fossil-bearing zone. A Pleistocene exposure 60 feet thick may include at least three distinct and successive faunas, each occurring at a certain horizon. Pleistocene fossil zones as a rule are only a few inches thick and are not everywhere separated by soil zones or definite erosional breaks. In some places they are separated by a lithologic change.

Since glacial studies indicate a succession of Pleistocene faunas in North America, a shifting of faunas should be recorded in the deposits in nonglaciated areas near the glaciated region. For such a study, work must be concentrated in a locality with extensive Pleistocene deposits both horizontally and vertically, in order to solve a number of the problems encountered in geographic correlations.

The following sequence of Pleistocene vertebrate faunas in such a locality (Meade and Seward counties, Kansas) has been worked out in the High Plains region in the past 11 years. The faunas are listed from oldest to youngest, and climatic conditions as interpreted from a study of these faunas are indicated.

Deer Park Fauna (*Cool*)

(Hibbard, 1938; 1944; 1949)

The earliest recognized cool-climate fauna in the High Plains was taken from the silts and clays of the Missler member of the Meade formation (Hibbard, 1949; not Frye, Swineford, and Leonard, 1948). The silts and clays overlie the Meade gravels of southwestern Kansas, in Meade County. The following forms constitute the Deer Park fauna:

MAMMALIA

Geomys sp.—Eastern pocket gopher
Procastoroides lanei (Hibbard)—Beaver (extinct)
Pliolemmus antiquus Hibbard—Lemming (extinct)
Pliopotamys meadensis Hibbard—Ancestral muskrat? (extinct)
Stegomastodon mirificus (Leidy)—Mastodon (extinct)
Nannippus phlegon (Hay)—Small horse (extinct)
Equus (*Hippotigris*) *simplicidens* Cope—North American zebra (extinct)
Camelops sp.—Camel (extinct)

The interpretation of cool climatic conditions is based upon the dominance of microtine forms in contrast to the dominance of cricetine rodents and other southern elements in the Rexroad fauna (Hibbard, 1938; 1941b) which was found less than three fourths of a mile from the Deer Park locality in the underlying Rexroad formation.

Cudahy Fauna (*Cool*)

(Hibbard, 1944; 1949)

The Cudahy fauna in Meade County, Kansas, was recovered from the Crooked Creek formation (Hibbard, 1949) which overlies the Meade formation. The fauna was taken chiefly from the silts below the Pearlette ash; a few forms were recovered from the extreme base of the ash, approximately 8½ miles northeast of the locality of the Deer Park fauna. The Cudahy fauna has been recovered from five localities in Meade County and is also known from Clark, Russell, and Lincoln counties, Kansas. The following forms are known:

INVERTEBRATES—numerous (*see* Frye, Leonard, and Hibbard, 1943; and Frye, Swineford, and Leonard, 1948).
PISCES—remains (unstudied)
AMPHIBIA—numerous remains (unpublished)
REPTILIA—remains (unpublished)
AVES—numerous remains (unstudied)
MAMMALIA

Sorex cinereus Kerr—Shrew
Sorex cudahyensis Hibbard—Shrew (extinct)
Neosorex lacustris Hibbard—Water shrew (extinct)
Microsorex pratensis Hibbard—Pigmy shrew (extinct)
Mustela sp.—Weasel
Citellus sp.—Ground squirrel
Geomys sp.—Eastern pocket gropher
Parageomys tobinensis Hibbard—Pocket gopher (extinct)
Reithrodontomys cf. *pratincola* Hibbard—Harvest mouse (extinct)
Peromyscus cragini Hibbard—Cragin white-footed mouse
Cudahyomys moorei Hibbard—Cricetine rodent (extinct)
Synaptomys (*Mictomys*) *borealis* (Richardson)—Boreal lemming mouse
Microtus paroperarius Hibbard—Tundra meadow mouse (extinct)
Microtus (*Pedomys*) *llanensis* Hibbard—Upland meadow mouse (extinct)

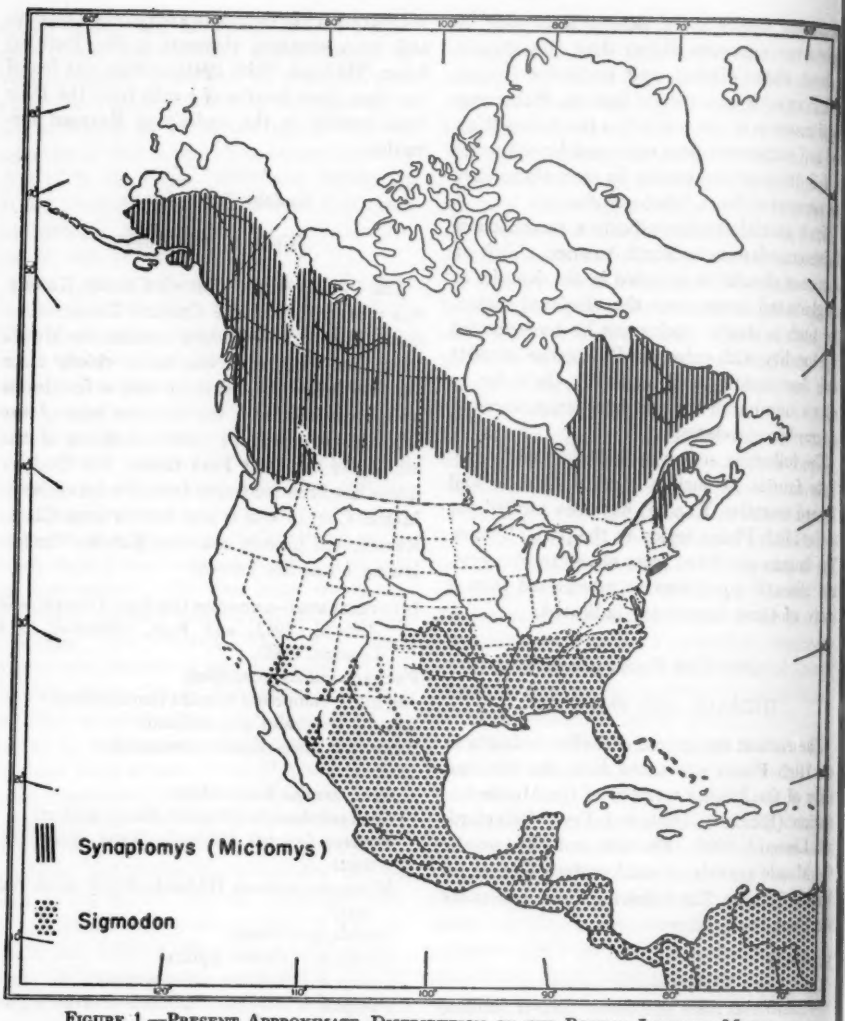

FIGURE 1.—PRESENT APPROXIMATE DISTRIBUTION OF THE BOREAL LEMMING MOUSE, *Synaptomys* (*Mictomys*)

Shown in contrast to the present distribution of the Cotton Rat, *Sigmodon*. The Boreal lemming mouse was common in the Cudahy fauna, while the Cotton Rat was abundant in the Borchers fauna.

Pitymys meadensis Hibbard—Vole (extinct)
Phenacomys sp.—Phenacomys
Ondatra kansasensis Hibbard—Little Great Plains muskrat (extinct)
Equus sp.—Horse

The Cudahy fauna seems to indicate the closing phase of a glacial age (Hibbard, 1944, p. 741–742). It is not certain whether this glacial fauna lived during a glacial age or whether these animals were the last survivors after the recession of the ice. The fauna is definitely Boreal in its affinities to living forms which are found from southern Canada north to Alaska. (See Figures 1 and 2 on which the present distribution of *Synaptomys* (*Mictomys*) *borealis* is contrasted with the present distribution of the

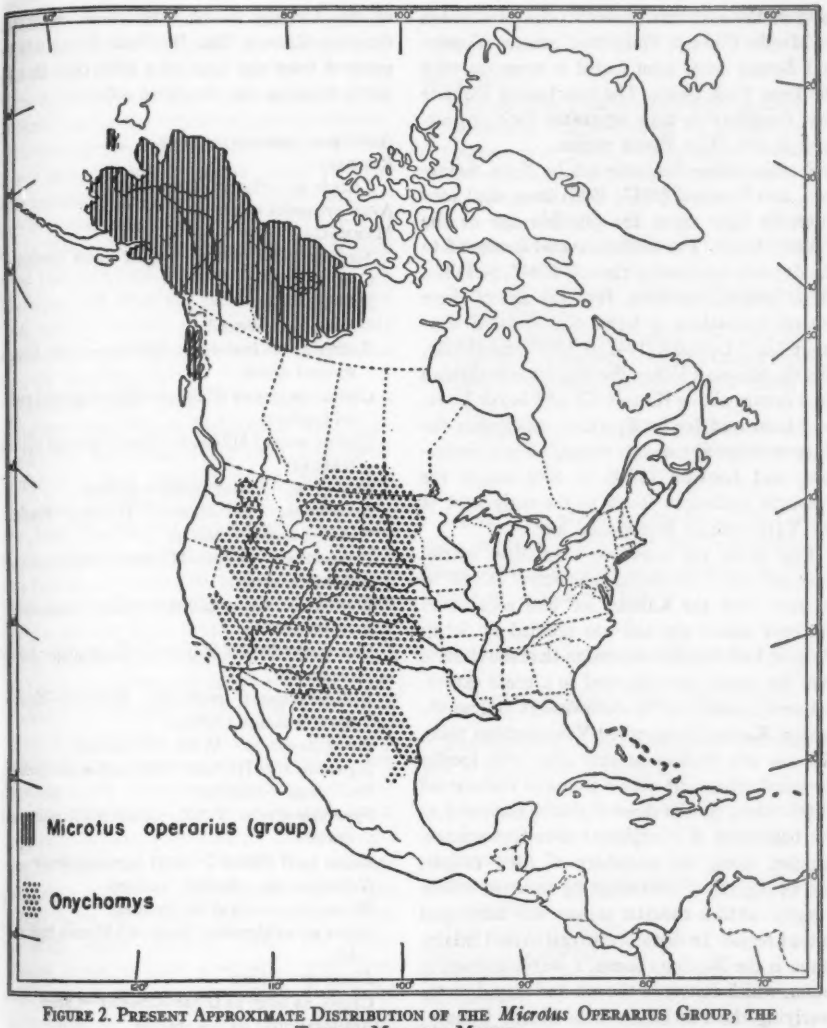

FIGURE 2. PRESENT APPROXIMATE DISTRIBUTION OF THE *Microtus* OPERARIUS GROUP, THE TUNDRA MEADOW MOUSE

In contrast to the present distribution of *Onychomys*, the Grasshopper Mouse. A close relative of the Tundra meadow mouse was common in the Cudahy fauna, while the Grasshopper Mouse was abundant in the Borchers fauna.

genus *Sigmodon* and the present known distribution of the Operarious group of *Microtus* is contrasted with that of the genus *Onychomys*.) *Synaptomys* (*Mictomys*) *borealis* is a common element of the Cudahy fauna and now lives in the Boreal region. *Microtus paroperarius* was abundant in the Cudahy fauna; though the species is extinct, the group of microtines to which it belongs now lives in the Arctic region. The genus *Sigmodon* and the genus *Onychomys* were two of the abundant elements in the Borchers fauna which occurred in the same area after the extinction of the Cudahy fauna. The above four forms give a fair and contrasted picture of

most of the elements known in the two faunas in Meade County. Only two genera (*Geomys* and *Equus*) have been found in common with the Deer Park fauna. The two faunas indicate that considerable time separates their appearance in the High Plains region.

Studies of the Pearlette ash by Frye, Swineford, and Leonard (1947; 1948) have shed considerable light upon the possible age of the Cudahy fauna. The authors stated in regard to the deposits containing the ash (1947, p. 1182), "It is judged, therefore, that the age of these several formations is latest Kansan and Yarmouthian." Leonard (1947, p. 1202) stated that, "In the Missouri Valley the Pearlette molluscan zone occurs above Kansas till and below Loveland loess and Iowa till, which establishes the Yarmouthian age of the fauna." Frye, Swineford, and Leonard (1948, p. 506) assign the Pearlette molluscan fauna to the early part of the Yarmouthian interglacial age.

This raises the question, when does glacial time end and interglacial time start? It will be granted that the Kansan ice had receded in the area where the ash was studied in South Dakota, but this does not mean that the climate over the region had changed to a great extent. A Boreal fauna lived in southwestern and north-central Kansas in so-called Yarmouthian time. We are not dealing in this case with locally stranded relics, but with a fauna of widespread distribution. At the close of glacial time and at the beginning of interglacial time forms intermingled along the periphery of their ranges, and all degrees of intermingling occurred within a region until a climatic climax was developed in that region. In distinct contrast to the Cudahy fauna is the Borchers fauna, a warm-temperate fauna, which occurs in the silt and clay directly overlying the Pearlette ash in Meade County, Kansas. Here we are dealing with the same geographic locality and the same formation though later and under different climatic conditions.

Borchers Fauna (Warm)

(Hibbard, 1941a; 1942; 1943; 1949)

The Borchers fauna was recovered from the Crooked Creek formation, approximately 5½ miles southwest from the locality where part of the Cudahy fauna was taken in Meade County, Kansas. The Borchers fauna was recovered from the base of a silty clay that directly overlies the Pearlette ash.

AMPHIBIA—remains common
REPTILIA
Testudo sp.—(Large) Land turtle
AVES—remains abundant
MAMMALIA
Sorex taylori Hibbard—Taylor shrew (extinct)
Canis sp.—Dog
Felis sp.—Cat
Mustela sp.—Weasel
Spilogale cf. *leucoparia* Merriam—Rio Grande spotted skunk
Citellus meadensis Hibbard—Meade ground squirrel (extinct)
Citellus cragini Hibbard—Cragin ground squirrel (extinct)
Geomys sp.—Eastern pocket gopher
Perognathus pearlettensis Hibbard—Pearlette pocket mouse (extinct)
Perognathus gidleyi Hibbard—Gidley pocket mouse (extinct)
Etadonomys tiheni Hibbard—Heteromyid rodent (extinct)
Onychomys fossilis Hibbard—Grasshopper mouse (extinct)
Reithrodontomys pratincola Hibbard—Meadow harvest mouse (extinct)
Parahodomys sp.—Wood rat (extinct)
Sigmodon hilli Hibbard—Hill cotton rat (extinct)
Ondatra sp.—Muskrat
Synaptomys vetus Wilson—Ancestral lemming (extinct)
Zapus burti Hibbard—Burt jumping mouse
Nekrolagus sp.—Rabbit (extinct)
Hypolagus sp.—Rabbit (extinct)
Lepus cf. *californicus* Gray—California jack rabbit
Equus sp.—Horse
Camel, as large as *Gigantocamelus*—Camel
Antilocapridae sp.—Antelope

When the Borchers fauna lived in that region, the climate was as warm as it is at present, or warmer. The fauna as a whole is related to the recent fauna of southwestern North America. It appears to have lived near the optimum conditions of an interglacial time. Unfortunately no molluscan remains were found associated with the vertebrates, nor are they known from this horizon in the Pleistocene deposits unless the Rezabek fauna of Lincoln County, Kansas, is

an eastern lowland fauna of equivalent age (Hibbard, 1943b). The only known form common to the Borchers fauna and the Cudahy fauna is *Reithrodontomys* cf. *pratincola*. It is of interest to note the return of some genera and even some species common to the region when it was occupied by the warm upper Pliocene Rexroad fauna. This is the first known appearance of these forms in the region since the shift of the Rexroad fauna. When the interglacial fauna that occupied the area prior to the Cudahy fauna and after the recession of the Deer Park fauna is found, it should contain more forms in common with the Rexroad fauna than does the Borchers fauna.

The Hay Springs fauna of Nebraska was one of the first High Plains Pleistocene faunas collected. The fauna has never been completely studied as a unit, though many faunal lists have been published (Matthew, 1902; 1918; Hay, 1924; Schultz and Stout, 1948). The fauna may represent an assemblage from one Pleistocene horizon, or it may be a faunal complex of Pleistocene mammals from more than one horizon. Schultz and Stout (1948, p. 566) state that it is of possible late Kansan or Yarmouth age and that *nearly all* of the fossils come from below the marl-peat bed and Pearlette ash. The faunal list represents an interglacial fauna. The presence of *Microtus pennsylvanicus* (Ord) in the collection of the American Museum from this fauna indicates that the Hay Springs fauna complex is, in part, post-Cudahy fauna in age. Most of the forms listed for the Hay Springs fauna show a closer relationship to the Cragin Quarry fauna than other known faunas from the High Plains (Rinker, 1949). The fauna appears to be, in part, equivalent to the Rezabek fauna. A definite correlation cannot be made owing to the unknown vertical range of Pleistocene forms and the unknown stratigraphic position of the forms recovered. Its relationship to other known faunas is therefore questionable.

Cragin Quarry Fauna (*Warm*)

(Hibbard, 1939; 1949)

The Cragian Quarry fauna was taken from an old artesian spring deposit of Pleistocene age younger than the deposits containing the Borchers fauna in Meade County, Kansas, 2½ miles from the locality of the Cudahy fauna.

MAMMALIA
- *Aenocyon dirus* (Leidy)—Dire wolf (extinct)
- *Smilodon* sp.—Saber-toothed cat (extinct)
- *Panthera atrox* (Leidy)—Giant jaguar (extinct)
- *Felis* cf. *oregonensis* Rafinesque—Mountain lion
- *Geomys* sp.—Eastern pocket gopher
- *Lepus* sp.—Rabbit
- *Mammuthus columbi* (Falconer)—Columbian elephant (extinct)
- *Paramylodon harlani* (Owen)—Harlan ground sloth (extinct)
- *Equus francisci* Hay—Francis horse (extinct)
- *Equus niobrarensis* Hay—Niobrara horse (extinct)
- *Camelops kansanus* Leidy—Kansas camel (extinct)
- *Tanupolama* sp.—Llama-like camel (extinct)
- *Breameryx minimus* (Meade)—Meade antelope (extinct)

On the basis of the occurrence of the Columbian elephant, sloth, and the pronghorn, the fauna is considered to have lived in the region during an interglacial time.

Jones Fauna (*Climatic conditions intermediate*)

(Hibbard, 1940; 1942; 1943a; 1949)

The following Jones fauna was found near the top of the Vanhem formation.

MOLLUSCA (*See* Goodrich, 1940)
PISCES—unidentified
AMPHIBIA
- *Ambystoma tigrinum* (Green) (Tihen, 1942) Tiger salamander
- Frog and toad remains

REPTILIA—unstudied
AVES—(Downs, in ms.)
MAMMALIA
- *Sorex cinereus* Kerr—Shrew
- *Mephitis mesomelas* Lichtenstein—Striped skunk
- *Taxidea taxus* (Schreber)—Badger
- *Citellus richardsonii* (Sabine)—Richardson ground squirrel
- *Citellus tridecemlineatus* (Mitchill)—Thirteen-striped ground squirrel
- *Cynomys ludovicianus* (Ord)—Prairie dog
- *Geomys* sp.—Eastern pocket gopher
- *Perognathus* sp.—Pocket mouse
- *Onychomys leucogaster* (Wied)—Grasshopper mouse
- *Peromyscus* sp.—White-footed mouse

Microtus (*Pedomys*) *ochrogaster* (Wagner)—Prairie meadow mouse
Microtus pennsylvanicus (Ord)—Eastern meadow mouse
Camelops sp.—Camel (extinct)
Platygonus sp.—Peccary (extinct)

These forms are all modern in aspect (except *Camelops* and *Platygonus*) though *Microtus pennsylvanicus*, *Sorex cinereus*, and *Citellus richardsonii* are no longer found living in Kansas but now live much farther north and northwest. Their presence in the deposit indicates a cooler and slightly more humid condition than the present. The fauna may have lived in the region after the Wisconsin ice sheet had begun to shrink.

Speciation during the Pleistocene

Much has been written on the lack of development of new forms during the Pleistocene because of the short duration of that epoch. As can be seen from the above faunas, each shift brought new forms into the region, but few of these are immigrants from other continents. Not enough is known of any one species to trace its phylogeny through the Pleistocene. It is evident that considerable speciation as well as extinction did take place during the Pleistocene (Gazin, 1942). To speculate upon the problem is like trying to walk on the thinnest of ice; at least 15 genera of the modern North American land mammals north of the Mexican boundary are unknown from Cenozoic deposits although they must possess a long geologic history.

Need for Pleistocene Paleontologists

With improved methods in collecting from Pleistocene horizons, such as sifting and washing of matrix, there has been built up a large backlog of invertebrate, fish, amphibian, reptile, bird, and mammal remains most of which must occupy storage space in numerous museums until specialists in these fields are available.

A study of these remains would considerably enrich and advance our knowledge of the life of the Pleistocene and of the dispersal and speciation of our Recent faunas.

All this knowledge is essential in the correlation and dating of Pleistocene deposits. Once the glacial, interglacial, and nonglacial deposits are correlated, the relative chronology of the Pleistocene will be known, and in the future can be placed in its proper position against the yardstick of an absolute chronology. Furthermore, it will settle the problem of the Pliocene-Pleistocene boundary.

Pliocene-Pleistocene Boundary

In a report on the Pleistocene studies of North America at the present time, the question of the Pliocene-Pleistocene boundary problem cannot be ignored. Those interested in the controversy are referred to the *Pleistocene of the Great Plains* (Colbert, 1948).

Owing to the fact that the Benson fauna of Arizona, the Blanco fauna of Texas, the Rexroad fauna of Kansas, and other faunas of equivalent age are pre-Nebraskan, they are not included in the present discussion of the Pleistocene faunas of North America. The fauna from the Broadwater of Nebraska has not been described and therefore cannot be definitely correlated with other faunas.

Until the faunas and deposits are well enough known in North America to allow a sound correlation of glacial deposits with nonglacial deposits, and the correlation of Pleistocene faunas from the High Plains with Pleistocene faunas from eastern and western North America, any attempt to correlate American and European Pliocene and Pleistocene faunas is futile.

Conclusions

The work done in Pleistocene Vertebrate Paleontology in North America during the past 15 years has been emphasized. Throughout this period an increasing number of students have contributed to our knowledge of Pleistocene vertebrates. Common interests have developed among Pleistocene geologists, anthropologists, paleobotanists, members of the Ground-Water Division of the U. S. Geological Survey, and members of the Soils Research Division of the U. S. Department of Agriculture. This cooperation has made possible many of the recent contributions; furthermore, it has stimulated and helped to initiate new approaches to the study of Pleistocene deposits and their contained fossils.

Great progress can be predicted in faunal

studies, in paleoecology, and in the correlation of Pleistocene faunas for the future in North America, as well as a better understanding among the various specialists in related fields, with a close intergradation of related facts.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

5. GLACIAL EROSION AND SEDIMENTATION

By Chauncy D. Holmes

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Introduction

As in many other phases of geologic study, problems of glacial erosion and sedimentation have a twofold nature. One aspect is concerned largely with areal description of deposits and topographic forms attributed to glaciation. The other aspect deals with search for principles of glacial erosion and deposition by which the deposits and topographic forms have originated. While these two aspects are so closely related as to be virtually inseparable, the latter is of greater fundamental significance than the former, although knowledge of the principles of glaciation rests mostly on accurate observation and description of the field evidence. Field evidence, however, has generally been interpreted in terms of principles already accepted by the investigator, and descriptive terminology has been selected accordingly. This may be standard procedure, but its application to glacial features is decidedly more hazardous than is the case with either fluvial or eolian features. Erosion and deposition by streams and wind can be studied at close range both in the field and in the laboratory, but observation of processes beneath moving ice a few hundreds or thousands of feet thick may forever remain as impossible as observation of metamorphism beneath a developing mountain range. Laboratory studies on the nature of ice give many clues to the probable behavior of glacier ice where erosion, for instance, has taken place, but the amount of extrapolation thus involved emphasizes the need for caution and for confirmatory evidence. Careful distinction among hypothesis, theory, and demonstrated principles is essential.

The present paper directs attention especially to some of the more recent contributions to the principles of glaciation. For discussions of areal studies, readers are referred to the excellent summaries by Flint (1947) and by Woldstedt (1929).

Glacial Erosion

Historical Summary

In the early days of the present century, opinion among glacial geologists became sharply divided on the subject of whether glaciers, particularly continental glaciers, did or did not effect much erosion. In 1905 Fairchild stated the extreme view of the nonerosionists by declaring "the ice-erosion theory a fallacy", though he admitted a certain amount of abrasion or smoothing of bedrock surfaces by the passage of the great glaciers. Even regarding erosion by valley glaciers, some investigators have suspected that rills of meltwater beneath the ice,

pressed and repeatedly diverted by forward ice motion, could account for much of the valley deepening ascribed by others to glacial erosion. Because of conflicting interpretations of evidence, most geologists have adopted the view that glaciers effect considerable erosion "under favorable conditions." Current study and research are still seeking to determine what constitutes favorable conditions.

Early studies of glacial erosion were greatly handicapped by erroneous concepts regarding the principles of glacier movement. Until the present decade, most investigators based their interpretations of glacier activity on the unwarranted assumption that the basal parts of a continental glacier were relatively slow moving or stagnant because of their load of drift, especially in areas of appreciable topographic relief. Thus a glaciated plateau was regarded *a priori* as having undergone, in general, more erosion on the hilltops than on the valley floors. The few papers opposing this view in the 1920's and 1930's received scant recognition. The outstanding recent contribution to this field is the work of Demorest (1938; 1942). His thorough analysis of the mechanical principles involved in glacier movement is supported by ample field evidence. Rate of plastic yielding of the ice increases with depth, and the basal zone of a glacier is much more mobile than was generally supposed. Especially in continental glaciers, the chief movement of ice toward the glacier margin is by a squeezing out of the basal ice from beneath the weight of ice above it. This principle of extrusion flow affords a promising approach to the solution of many problems in glacial erosion, transportation, and deposition.

Many of the concepts regarding glacier movement which Demorest has so ably elucidated have long been accepted by at least some worker (Geikie, 1895, p. 200–201), though the subject had lacked thorough and comprehensive formulation. Outside the United States and Canada, war conditions have delayed somewhat the recognition of Demorest's contributions. However, European workers are now informed through the medium of the newly organized British Glaciological Society. This society will undoubtedly prove to be a most important medium of international communication on all phases of glaciologic study.

Modes of Glacial Erosion

Present workers agree in general that removal of joint-bounded blocks of bedrock is quantitatively more important than bedrock abrasion, though the actual amounts can only be inferred. The evidence, however, comes from glacial-erosion features (Jahns, 1943) and from the stony nature of the drift in many places.

Glacial erosion is notably selective, and in most instances the reasons for this selectivity are obscure. Along a typical glaciated valley, for example, short but steep descents alternate with relatively longer segments of gentle (or even reverse) gradient, making the so-called stair-step profile. Some investigators explain this profile as the expression of notable differences in either lithology or structural features such as jointing, or both. Other investigators have failed to find these controls or have regarded them as inadequate. With adequate structural control, the "risers" of the stair-step profile should remain stationary as valley deepening goes on; but, without structural control, these declivities should either disappear or migrate upvalley by sapping or block removal. Probably most students accept the doctrine of structural (joint) control advocated by Matthes (1930), though the present writer suspects that this explanation is only a first approximation to the truth. Cotton (1941) favors the view that both abrasion and some form of subglacial sapping have played significant parts in the development of most "stepped" valley profiles.

Block removal is commonly referred to as glacial quarrying or glacial plucking, though in most cases without clear explanation of the mechanics involved other than simple shoving. Rigid ice may effect an enormous amount of shoving, as has been observed along the borders of some valley glaciers, but the increasing weight of evidence that deep erosion has occurred where the basal ice must have been unusually plastic shows the need for renewed search to discover other possible means of bedrock disruption. Most believers in the plucking hypothesis probably assume the mechanism clearly stated by Cotton (1941, p. 121). The glacier ice freezes to "loosely held joint-bounded blocks of rock (water passing readily into ice at freezing temperature wherever tension is developed)

and the blocks are dragged away." To be effective, this mode of erosion is believed to involve some additional assumptions. (1) The ice thus adhering to the block must have considerable rigid continuity with the moving ice above it in order to transmit the necessary tractional force. The amount of tractional force available may be a resultant function of the rate of glacier movement forward on the one hand and, on the other hand, the rate at which the ice could yield plastically to the stresses thus set up. (2) The tensile strength of the ice must be adequate. (3, vitally important) The heat set free in freezing must be removed, presumably by conduction. (4) Probable freezing of ice to an adjacent immovable rock mass would necessitate differential movement within the rigid, tension-stressed ice, either by differential flow or by shear-plane gliding. This is to permit the prism of ice with its attached block to move forward past the adjacent and equally rigid ice on either side.

Stress conditions implied by the expression "development of tension" may be better interpreted as merely a local condition of relatively lower pressure. This latter view emphasizes the existence of a pressure gradient. Thus, instead of appealing to traction on the front of a block which happens to face into the zone of lower pressure, the possibility of pressure from the rear should receive careful attention. Carol (1947) has recently observed the plastic flow of ice past a bedrock knob beneath a small glacier in the Alps. Though because of the thinness and rigidity of the ice the observed conditions were not comparable to those at great depth, Carol suggests that water from pressure melting on the stoss side might move along the joints in the rock and refreeze on encountering reduced pressure near the lee side, thus forcing away the joint-bounded blocks. This appears to be a promising hypothesis. If the joints are sufficiently open, ice may enter them directly as interpreted earlier by Martin (1927), who described till-filled joints in limestone at Kinnekulle, Sweden.

Conduction of heat from the Earth's interior is believed to be a potent factor opposing extensive bedrock disruption by regelation along joints. Normally, beneath a deep glacier, the rock temperature is presumed to increase downward, beginning from the temperature of pressure melting at the glacier floor. Holmes (1944) has suggested that block removal at places of deep glacial erosion may have been facilitated by downward percolation of water from pressure melting or from other possible sources, which would lower the temperature of the subjacent rocks and permit easy regelation in the joints along the glacier floor. The rocks also must store and release heat in response to pressure melting and regelation of the ice in contact with them.

Erosional Topography

In addition to the characteristic erosional forms already mentioned, a few others, including cirques, have received notice in the recent literature. The notable steepness of the cirque wall is believed due to sapping at the base where the joint-bounded blocks are probably not "loosely held." Processes of block removal within the bergschrund (crevasse between glacier and cirque headwall, which opens up each spring or summer) are essentially comparable to those at the surface where atmospheric temperatures can function. However, much headwall sapping has evidently gone on far below the depth to which the bergschrund would extend, and the processes there may well be the same as those by which the valley-profile steps are believed (by some) to recede.

In recent discussions of the cirque-wall problem, Lewis (1940; 1949) has stressed the possible role of surface-derived meltwater which flows into the bergschrund in summer. His statement of temperature equilibrium between ice and meltwater is well expressed, and he suggests that freezing of this water is a chief process in cirque-wall recession. However, he apparently ignores the all-important matter of heat removal necessary to cause such freezing beneath the ice cover where air circulation is impossible.

Glacial erosion of bedrock is generally believed to result in the *roches moutonnées* type of topography (numerous rounded bedrock knobs), whether brought about by valley, piedmont, or continental glaciers. A disputed question is whether such a surface represents the maximum depth to which the eroding ice could excavate because of lack of sufficient joints in the rock, or whether that surface develops early in the

process and is merely a characteristic of glacial erosion without being an indication that the glacier had reached its ultimate in bedrock erosion. The characteristics of *roches moutonnées* most commonly mentioned are the strongly abraded stoss sides and the uneven lee sides evidently shaped by block removal. Significantly, these manifestations of glacial erosion represent destruction of the forms rather than their creation. Their presence suggests an earlier phase of block removal which has left the rock knobs as prominences among the sites of deeper erosion. The two phases of erosion probably develop together, and recognition of both seems desirable.

Several occurrences of glacial bastions (bedrock salients in a main valley at tributary junctions) in Colorado have been noted by Ives (1946), who believes this type of land form may be more widespread than is now realized. Ives suggests that failure of the main glacier to widen its valley at these tributary junctions is due to shoving of the main glacier away from the proximal valley wall by thrust from the entering tributary. This interpretation apparently assumes a high degree of ice rigidity in both the main and tributary glaciers, and valley deepening mostly by abrasion. The present writer believes that other hypotheses might profitably be considered.

In nearly all regions, topographic irregularities seem to have influenced strongly the local directions of movement of the eroding glaciers, where presumably the basal ice was moving by extrusion flow. However, at certain localities in Canada, striae and glacial grooving extend in a nearly constant direction without apparent influence from either topography or structure (Bateman, J. D., personal communication; Smith, 1948). How the conditions of glacier movement in these instances differed from those at other localities has not been explained.

Striae on bedrock surfaces have long been the standard guide to direction of glacier flow. However, where movement of the basal ice was subject to strong topographic control, glacier movement may seem to have been equally possible in either direction. Also in many cases confirmatory evidence is highly desirable, as is shown by the interpretation (Clark, 1937) that, near the New England-Canadian boundary, a late Wisconsin glacier moved northward toward the St. Lawrence lowland. Striae made by this ice could well be taken as indicating southward flow. Friction cracks in the bedrock (Harris, 1943) may provide the necessary confirmation. These cracks are characteristically crescent-shaped spall scars, many of them imperfect, caused presumably by pressure from boulders pressed downward and forward as the glacier moved them along. Some of the crescentic forms are convex in the downcurrent direction, while others have the reverse orientation. The diagnostic feature common to both is the forward or downcurrent dip of the basal fracture surface. As these fractures are much deeper than striae, they are generally legible long after the accompanying striae are too faint for positive interpretation.

Glacial Sedimentation

Historical Summary

Most glacial deposits occur as land forms so strikingly different from those characteristic of aqueous deposits that many investigators have been satisfied to study only the physiographic aspects of these deposits. While in many instances and for many purposes the topographic expression of glacial deposits is an adequate basis for their classification, this emphasis on land form has diverted attention from study of the sediments themselves and has encouraged superficiality and false assumptions. Until recently the study of glacial sediments has lacked the stimulus of strong economic demands, and the predominantly pure-science aspect of the field has attracted relatively few workers. However, the present strong and increasing demand for gravel in the construction industries and in road building has accompanied more critical analysis of structural foundations and more intensive study of soil properties and origins. In glaciated territory these activities involve glacial features directly and have given impetus to the study of glacial deposits primarily as sediments. This present trend is a long-delayed return to the line of approach followed by many pioneer investigators.

Nature of Drift

Recent thought on problems of interpreting glacial sediments recognizes that, in the matter

of size sorting, glacial deposits constitute a complete gradational series ranging from the characteristic heterogeneity of till to the best of size sorting and stratification which moving water has produced (Flint, 1947). Even though most till exposures give no obvious indication of water action, any sediment deposited by glacier ice must be set free by melting. Therefore all ice deposits have accumulated in the presence of at least a thin film of meltwater which may have removed (or added) some of the finer grade sizes. This can hardly be classed as a recent discovery, though the concept remained obscure for many years. The usual distinction between till and stratified (size-sorted) drift is in certain cases necessarily arbitrary, though it is essential for purposes of study and discussion.

As melting and deposition of drift are believed to occur throughout a zone extending some miles back from the glacier margin, the meltwater must ultimately find its way out from beneath the ice. Local and temporary concentration of meltwater flow under these conditions has apparently brought about enough size sorting to develop the pockets or lenses of sand and gravel now encased in the till, which some authorities prefer to regard as "boulders" derived from an overridden outwash deposit. Deformation or steep tilting of the stratification planes observed in many of these gravels seems best explained as due to contemporaneous glacier movement. Under the "boulder" hypothesis, one must explain how these masses could have been carried and deposited intact while the ice matrix or "cement" was in temperature equilibrium with the surrounding ice and therefore just as plastic as the transporting medium from which they finally escaped.

Till Fabric

Another important fact which has recently emerged from half a century of obscurity is that till has an inherent and easily recognized organization conveniently referred to as till fabric (Holmes, 1938; 1941). The imbedded stones have statistically preferred orientations with respect to the direction of flow of the ice from which they were deposited. Preferred orientation of the stones is influenced to some extent by their shapes and degrees of roundness. It affords many clues to the conditions attending deposition and records the direction of glacier flow while the component fragments were being released from the ice.

As Flint (1947, p. 107) has stated, the study of till fabric involves arduous and painstaking effort, but it offers a relatively new field of geologic research from which significant results may be confidently expected. It has already found practical use in Finland (Hyyppa, E., personal communication; Okko, V., personal communication). Recently Lundqvist (1948) has compared stone orientation in till and other types of deposits including solifluction masses. He concludes that orientation is a distinct aid in working out the history of a deposit, but that it must be used with caution.

Depositional Types

Correct interpretation of the effects of continental glaciers requires the mapping of glacially produced features on a continental scale. For North America, the progress of this work is admirably summarized and represented on the Glacial Map of North America (Flint and others, 1945). No comparable map of European glaciation exists, though preliminary inquiry is under way by members of the Committee on Interrelations of Pleistocene Research. A similar map or summary for South America also is needed. As for the Asiatic regions, prospects for adequate data of this kind within the near future seem dubious, though such data are equally desirable.

Much detailed work in North America is still needed, especially in the vast area adjacent to Hudson Bay where the glacial geology is barely outlined even by reconnaissance surveys. However, much recent progress has been made in connection with surveys organized primarily for other types of geologic work. Published results deal with such features as end-moraine and ground-moraine patterns, drumlins, and eskers, which can be studied effectively in part by the use of aerial photographs (Norman, 1938; Wilson, 1938a; 1938b; Sproule, 1939; Gwynne, 1942).

The logical assumption that all typical ground-moraine topographic features constitute a gradational series finds at least partial expression in the familiar term *drumlinized*. The commonly well-defined limits of typical drumlin

areas have perhaps discouraged emphasis of this possible gradation in topographic expression. However, in many places the characteristic swell-and-swale topography of the Midwest till plains borders closely on the type of surface often described as drumlinized. Furthermore, drumlins as strictly depositional forms grade into rock-cored drumlins, the extreme forms of which are believed to owe their shape chiefly to glacial erosion. In topographic expression, therefore, this depositional series begins with, and is akin to, these erosional forms of *roches moutonnées* aspect.

On a till-plain surface in Iowa, Gwynee (1942) has noted a mottled or reticulated pattern in which the transverse markings seem best interpreted as a series of end-moraine deposits. They are so inconspicuous as to be noted only with the aid of aerial photographs. This occurrence is therefore another type of merging of ground and end moraines commonly observed along the inner borders of many Midwestern end moraines. A much more pronounced form of annual recessional end moraine is the so-called washboard moraines well displayed in parts of Quebec (Norman, 1938).

Hitherto unknown or little-known areas of drumlins have been described recently from Michigan (Bergquist, 1942) and from British Columbia (Armstrong and Tipper, 1948). Another drumlin study in southern Ontario (Putnam and Chapman, 1943) supplements the much earlier investigations in the classic region of western New York and raises new questions regarding the manner in which the Lake Ontario Basin influenced the behavior of the drumlin-forming ice around its margins.

Paleoclimatic Inferences

Observers are likely to encounter anomalous types of deformation structures in outwash deposits. In northern Illinois, Sharp (1942) has observed zones of sandy silt and clay up to 6 feet thick which have become expanded and have been thrust upward, downward, and laterally, and are intruded irregularly into adjacent sand strata. Sharp believes this deformation is caused by freezing and thawing while the subjacent strata were perennially frozen. This implies rigorous climatic conditions in a glacier-free region. Somewhat similar deposits have been described (for example, Slater, 1926; Berkey and Hyde, 1911) in which the deformation is attributed directly to glacier ice.

Contrasting interpretations dealing with probable climatic conditions attending the last deglaciation in eastern North America have appeared recently, based on the occurrence and distribution of isolated kames. One interpretation (Cook, 1946) is that these gravel mounds signify deglaciation chiefly by evaporation under a cool and clouded sky. Gravelly sediment in superglacial ponds would be lowered to the ground by slow wastage of the ice sheet, with convection melting of the ice at the bottom of the pond. Water at 32° F., in contact with the ice, is lighter than water a few degrees warmer. The coldest water therefore rises and is replaced by water slightly warmer, thus melting the ice. The other view (Holmes, 1947) interprets the kames as due largely to the action of abundant meltwater and copious superglacial drainage resulting from strong insolation.

Some Needed Research Bearing on Glacial Erosion and Sedimentation

Most of the problems here listed have been implied in preceding paragraphs. The list is by no means considered as a complete catalog of needs in these fields.

(1) Further experimental work on ice deformation. This is a neglected field, perhaps because of the difficulty and expense of getting properly designed apparatus. Substitutes for ice cannot be expected to yield significant results. The search should be for principles governing the behavior of ice as it responds to differential pressures beneath a glacier many hundreds of feet thick.

(2) Thorough study of ground-water conditions around existing glaciers. The information sought should include the amount of glacier-derived ground water, its depth of circulation, and its influence on the geothermal gradient.

(3) Careful studies of rock jointing in areas of deep glacial erosion. Cirques and the large steps along glaciated valleys are among the favorable sites. The study should include equally careful and thorough investigation of jointing

along the valley walls between the steps—in fact, along the entire valley, with emphasis on minor as well as major joints.

(4) Critical analysis, based on extensive field observation, of rock properties or characteristics that govern relative resistance to glacial erosion. Resistance to abrasion and resistance to block removal must be carefully distinguished, bearing in mind that erratics of enormous size have been reported.

(5) Investigation of till fabric in many areas, and further comparison of this fabric with any fabric evident in landslide deposits, solifluction masses, and similar materials. Engineers are already studying in this field, but geologists need geologic interpretations rather than those made from the viewpoint of the engineer.

Similar fabric studies might prove useful in connection with excavation at archaeologic sites, as a means of detecting subsequent disturbance of the accumulated matrix materials. Later burial of objects would doubtless leave a fabric in the replaced covering different from that in the undisturbed deposit at the same apparent horizon.

(6) Restudy of glaciated areas where earlier mapping and interpretation of glacial features may not have been done systematically.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

6. CLIMATOLOGY OF THE PLEISTOCENE

By Helmut Landsberg

The only fact that can be stated without reservation regarding the relation between the Pleistocene glaciations and atmospheric conditions is that during various stages of this epoch surface temperatures in many regions were considerably lower than they are at present. It is uncertain whether this lowering of temperature over large areas of the surface of the earth was the cause of the various periods of glaciation or whether it was a consequence. The whole problem has been the subject of speculation, and it is questionable whether any of the numerous hypotheses advanced can be dignified by the designation "theory".

Geologists, geographers, meteorologists, physicists, and lately even a physical chemist have contributed ideas which try to unravel the cause-and-effect relationships between climate and glaciation. In critically reviewing these hypotheses, one is forcibly struck by the fact that each author has analyzed the question in the light of his own experience, and in most cases has disregarded knowledge accumulated in the neighboring fields. The co-operative effort which will be made through the NRC Committee on Interrelations of Pleistocene Research can serve to guide future research work along lines which will bring all the evidence together and focus it on the problem.

As in all sciences that deal with history, it is usually easiest to work from the present back to more ancient times. We have now available, as comparative material, approximately 50 years of world-wide meteorological observations. The coverage is reasonably good over the continents, but data from oceanic areas are still sparse. These oceanic data do not enable us to test climatic trends. This should be kept in mind because the oceans cover about five-sevenths of the earth's surface. Hence our discussions on climatic trends of the present time are essentially based on observations from land stations. These observations show a progressive warming since 1900, especially in latitudes higher than 40°. The investigations along this line cover a great many areas in the Northern Hemisphere, *e.g.*, North America (Kincer, 1946), Greenland (Hovmøller, 1947), England (L. F. Lewis, 1948; Manley, 1946; 1948), The Netherland (Labrijn, 1945), Sweden (Ångström, 1939), Norway (Hesselberg and Birkeland, 1940), U.S.S.R. (Rubinstein, 1947). Evidence of rising temperatures during the last few decades is too overwhelming to be disregarded, but some questions remain. One is whether the observational series are homogeneous. In many places equipment and exposure of the instruments have changed. Such changes could affect the magnitude of the trend. More important for inferences regarding times earlier in the Pleistocene is the question as to how sustained such a trend might be. Inspection of some of the earliest European instrumental records indicates that trends toward higher and lower temperatures of similar magnitude and several decades' duration have occurred in the past. Hence one might conclude that such ups and downs are just part of the pattern of the present climate and therefore insignificant, if one thinks in terms of geologic time. Kincer has recently presented some material which, he believes, indicates a reversal of the upward trend of temperature noted in the first four decades of the present century. One should, however, not discount the usefulness of

analysis of the data from the period of instrumental records for the problems of Pleistocene climates. These data may give us leads to the causes of climatic variations in general.

Even our oldest meteorological records cover only about 250 years—and that length of record is available from a very few stations only![1] Thus indirect approaches to appraise the climatic changes of longer epochs have to be used. Generally, these other methods are only qualitative, and it is difficult to correlate them with other pertinent phenomena. Perhaps most important is the evidence offered by glaciers, which have been retreating everywhere in the world since the latter part of the nineteenth century (Ahlmann, 1943).

Prior to the middle of the last century, for the preceding several hundred years, the best available evidence is archaeologic. According to Ahlmann (1943), this evidence, especially in the Sub-Artic regions of the Northern Hemisphere, indicates several periods of relative warming and cooling which have contributed to the spread and decrease of population in those areas. In the more moderate regions we have historical reports on crops and the limits of distribution of certain crop plants. As we go back in time the methods become more and more indirect. Tree rings have offered some suggestions on climatic conditions for the past 1000 years, although this evidence seems essentially restricted to inferences concerning precipitation values. Perhaps the most important conclusion is that there is some relation to the rhythms of solar activity. However, the samples which cover longer period of time are restricted to a few localities. These tests also lack sufficient chronological correlation over larger portions of the earth's surface. The same applies to the evidence furnished by pollen analysis and the distribution of various types of animals which are sensitive to temperature and/or precipitation changes.

[1] The stations with the longest uninterrupted record are: Paris, France (1664); Wroclaw, Silesia (1692); Berlin, Germany (1700); Upsala, Sweden (1722); Lund, Sweden (1723); Padova, Italy (1725); Leningrad, USSR, (1725). In North America the first uninterrupted series started in 1780 in New Haven, Connecticut. Interrupted series, some of which start earlier than indicated above, are of relatively small value in the investigation of climatic trends.

We are confronted with three major hypotheses on the climatic variations leading to the Pleistocene glaciations. The first, elaborated by Milankovitch (1930), bases changes in temperature on periodic variations of the solar radiation received in one hemisphere, because of changes of the axis of the earth due to precession, and of elements in the path of the earth around the sun. These computations have led to a curve purporting to show a chronology of approximately 600,000 years of climatic variations. Even hemisphere-wide diminution of heat supply cannot explain the observed geological facts of glaciation if the total heat supply for the earth as a whole is constant (Flint, 1947). In the light of present knowledge on atmospheric circulation this latter objection does not necessarily hold. Even for shorter intervals of time, changes in the general atmospheric circulation on one hemisphere almost immediately have repercussions on the other hemisphere. In fact, the East Asiatic-Australian monsoon circulation is one single cell system and causes substantial air movements across the equator. Recent studies on the general circulation of the atmosphere have shown that the air motions over the surface of the earth *form one indivisible whole* and any changes in one place will affect the remainder of the global circulation. Since it can be assumed that there has been in the recent geologic past an entirely unsymmetrical distribution of land and sea with regard to the equator, quite possibly a change of heat supply on the Northern Hemisphere would simultaneously affect also the Southern Hemisphere, and vice versa. For this reason the Milankovitch hypothesis cannot be excluded from consideration. The greatest weakness is the fact that neither the elements of the path of the earth nor of the precession motion are well enough known to permit accurate timing. In addition, the procedure of converting radiation energy into surface temperatures is still tenuous.

It may be apropos to quote here a translation from Ludwig Rueger (1948). (Some of the references quoted by him are not available to the author; they are listed in the bibliography under Rueger's name.) His evaluation of the state of affairs based on the recent German literature in the field, however, jibes closely with our own.

"A series of papers discuss the chronology of the Ice Age. Spitaler produced a chronology which is considerably at variance with that of Milankovitch. This has led to a controversy with Wundt who tries to show that Spitaler has used incorrect premises. The difference in the indication of years between Milankovitch and Spitaler are in several places more than 100%! From a physical point of view Wagner considers the contradiction between Milankovitch and Spitaler as unsolved. Schwarzbach from a geological point of view is very skeptical with regard to the diluvial chronology of Milankovitch and Soergel. This reticence, and in part opposition, which has also been reflected in the works of other authors, applies to the accuracy of the absolute chronology and also to the reasoning which considers radiation as the main cause of glaciation. We therefore find that the problem of diluvial chronology is still in full flux."

The second major hypothesis postulates changes in solar radiation. Present-day evidence suggests that there are at least short periodic changes in the extra-terrestrial intensity of solar radiation. This evidence, in part, is based on calculations which, in detail, are open to criticism. This applies especially to the determinations of the so-called "solar constant" (Abbott, 1935). However, some of these earlier calculations might soon be checked by more direct measurements taken at great altitudes from rockets. The observations of the past years indicate, however, that solar radiation actually fluctuates. It is less clear whether such fluctuations are anything but short-periodic, and it will take many years of observation before any long-term trends can be discovered. Investigations on the general circulation in the atmosphere also seem to point more and more toward solar influences upon the large-scale fluctuations that must have occurred in the past (Willett, 1947). In summary, the glaciation hypothesis postulating fundamental changes in the solar radiation, coupled with simultaneous formation of mountains, remains the strongest contender in the field, even though individual elaborations of this theme are open to question (Simpson, 1939). A variant of this hypothesis attributes the change of radiation received by the earth not to long-range fluctuations of the primary energy emitted by the sun but to effects caused by clouds of cosmic dust, which entered the solar system. By absorption, scattering, and reflection of solar radiation such dust clouds might affect the heat balance of the earth materially (Sucksdorff, 1938; Menzel, 1948).

One of the most recent hypotheses on the cause of ice ages points out certain flaws in the Simpson theory, and it does not start from an a priori long periodic variation in the solar radiation. This hypothesis, proposed by the late G. N. Lewis (1946), holds that the glaciation phenomena could well be explained on a thermodynamic basis by a "siphoning process", which brings water by evaporation from the oceans to the already glaciated areas. It envisages only relatively slight changes in surface conditions, which might be produced entirely by terrestrial phenomena and lead to "run-away" conditions.

It cannot be our task here to review all the pros and cons of the various hypotheses, but we shall, rather, point out some of the investigations that might profitably be carried out to help solve the overall problem.

There is still a great need for observing contemporary changes that may throw light on past climatic history. This involves not only following the trends of individual climatological elements, such as temperature, but also work on overall trends in the atmospheric circulation. In that respect, studies of the type started by Brier (1947) would seem to be of considerable importance. The material for this study is on hand in the Northern Hemisphere weather charts, prepared during the war by the U. S. Weather Bureau, in co-operation with the Armed Forces. These cover the period from 1899 through 1938. It is now contemplated to bring this material up to date and keep it current. The greatest deficiency in this line is the lack of a similar series of charts for the Southern Hemisphere, particularly in view of the possible effects of the general circulation in the Southern Hemisphere on the Antarctic Ice Sheet.

Some information on the changes in Antarctica might be obtained by comparative studies of the meteorological results of the earlier Byrd expeditions with the data collected by Operation "High-jump", and an evaluation of this material is now under way. In this connection, the detailed meteorological observations from the second Byrd expedition should be published at the earliest possible date[2]. The significance of these studies for new hypotheses on the Pleisto-

[2] Published while present paper was in press: Court, A. (1949) *Meteorological data for Little America III*, Mo. Weather Rev., Suppl. no. 48, Washington, D. C.

cene glaciation has been discussed recently by Manley (1948).

It should not be overlooked, however, that sporadic data collected on individual expeditions from this area are unsatisfactory for this type of climatic study. The real advances in this field will have to await establishment of permanent bases in Antarctica. Only if long records are available can we expect to obtain the necessary correlations with simultaneous fluctuations in sea and land ice in that area.

More information is also needed on actual fluctuations of solar radiation. Our knowledge of the actual changes in the "solar constant" is still doubtful. This applies also to the solar energy received by the earth in the radio-wave region and through corpuscular radiation. This type of energy received from the sun is apparently absorbed in the high atmosphere. It is unknown how much these radiations contribute to the energy budget of the atmosphere. At present their fluctuations can only be indirectly arrived at by observations of the earth's magnetic field, variations of the ionosphere, and studies of the solar corona. There have been claims of an influence of these radiations at least on the day-by-day variations of weather (Arctowski, 1941; Abbot, 1935; B. and G. Duell, 1948).

Another series of observations that in the long run may throw some light on this question is the accurate measurement of sea levels. These would be needed to obtain data for correlation with recession of glaciers.

It is also essential to obtain a synoptic picture of all the indirect observations. This means that the climatic conditions inferred from tree-ring data, archaeological data, data on pollen analysis, and data on thermally sensitive animals be plotted for *simultaneous* periods on world-wide charts. From these charts the general circulation of earlier periods might be inferred, and differences from the present period might be obtained.

Surface data alone will not tell the whole story. Contrary to previous ideas, the influence of surface glaciation on the general circulation is not as significant at was once thought. Recent analyses of the circulation in the Greenland area have shown that it is not the ice cover that changes the circulation (Dorsey, 1945), as has been assumed by Hobbs (1945; 1948) and others. A critical review of Hobbs' ideas with many literature references has been published by Matthes (1946). The influence of the ice sheet is restricted to the relatively low layers of the atmosphere, especially as regards the amount of precipitation. The circulation of higher levels of the atmosphere is the significant factor. The complete mechanism of interaction of low-level weather conditions and circulation in the higher atmosphere (above about 10,000 feet) in a glaciated region is not known. Little thought has been given to the problem of how one might reconstruct the circulation in higher atmospheric levels prior to the period of instrumental observations.

Observations of the distribution of ash, from active volcanoes, which has been transported by currents at high levels, may contribute to the solution of this problem. This presupposes that individual specimens of ash could be recovered and traced back to a volcano active at the particular time. At least in oceanic-bottom sediments some evidence of such thin layers of volcanic ash can possibly be used to trace high-level wind direction at the time of deposition.

The one point that must be emphasized is the necessity of obtaining simultaneous observations at many points which will give some indication of the general global weather conditions at a particular instant. Isolated observations have very limited significance. Present-day microclimatic investigations indicate that within small distances climatic conditions, especially temperatures, can change radically and result in entirely different plant associations in close proximity.

It may also be possible to obtain some valuable information by systematic laboratory experiments on hydrodynamic and thermodynamic models. Attempts have been made to obtain flow patterns in various media with immersed heat and cold sources. Such experiments have been carried on in the Hydrodynamics Laboratory of the Department of Meteorology of the University of Chicago. Such experiments might be extended to various assumed models of paleoatmospheric circulation. The greatest drawback to these experiments is that the heat exchange effected by the hydrological cycle in the atmosphere has to be

neglected. However, the possibilities of model studies even along these limited lines should not be overlooked. The production of an "ice cap" in the laboratory might lend considerable weight to any of the thermodynamic hypotheses proposed.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

7. OLD-WORLD PALAEOLITHIC ARCHAEOLOGY

By Hallam L. Movius, Jr.

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"It is first and always essential to appreciate that prehistory is not, and never can be, a Science. Certain of the methods employed may be basically related to those used for the Natural Science, while the whole is directed towards the revelation of truth; yet the material upon which our evidence is based is of such a nature that it cannot be expected to yield absolute truth. Our research is a process of approximation, not of exact assessment. Man is an animal with powers of independent thought and invention, and with a free will. Through the constant use of clothing, tools, housing and common sense, he is the most adaptable creature in the face of static and changing climates."

A. J. H. Goodwin

Introduction

During the last century—ever since the first volume of Boucher de Perthes' *Antiquités celtiques et antédiluviennes* was published in 1846—significant and important discoveries of chipped-stone implements demonstrating the existence of man contemporary with an extinct fauna have been made at an ever-increasing tempo. Today, the "rate of discovery" is proceeding at a hitherto unrivalled pace. Whereas the early work on the succession of cultures during Old Stone Age times was confined in the main to evidence secured in Western Europe and immediately adjacent regions, in the last 25 years the existence of early man pretty well throughout the vast continental areas of Asia and Africa has been demonstrated likewise. The fact that the "classic sequence" established in Western Europe by De Mortillet was not necessarily applicable in these latter regions is now abundantly clear to the majority of workers. Indeed, during prehistoric times, just as in the historic period, environmental and geographic factors have played a dominant role in conditioning the behavior of various early (or primitive) groups of mankind. For, from the point of view of the development of man's material culture,[1] these factors, including climate, soil, flora, fauna, natural resources, and

[1] Some anthropologists maintain that culture is intangible—a particular kind of behavior, or various forms of behavior. For purposes of the present paper, however, the term is used with reference to assemblages of finite objects; these rather than psychological and sociological factors constitute the only record available to prehistoric archaeologists, whose concern is the study of extinct cultures. Indeed, with reference to the study of the prehistoric cultures of the Old World, that field of the social sciences to which archaeology belongs offers no alternative at present. Although the prehistorian may suspect that certain patterns of behavior have moulded and conditioned the development of a given Stone Age culture, our knowledge to date is far too imperfect and fragmentary to prove it. Therefore, the study of the archaeological record must be conceived of as history shorn of all but its imperishable material culture traits; however, in that it deals with groups of mankind at a primitive level of subsistence and without written record, prehistoric archaeology is even more closely allied to ethnology.

topography, must be considered as having provided the stage—scenery, backdrops, lighting, etc.—on which the human drama has been played ever since the emergence of the first primitive hominids from the ancestral, paleoanthropoidal stock. But the *rate of change*, and the *degree of interplay* between man's cultural achievements and the environment to which he was ever struggling to adapt himself, and on which he was dependent for his livelihood, has been far from constant.

Even a very superficial survey of the literature covering prehistoric archaeology in the Old World discloses the fact that the reaction of our Stone Age forebears to changes in stage and setting, which repeatedly occurred throughout the Pleistocene, has not always proceeded at a uniform or even predictable rate. From the beginning of Upper Palaeolithic times, the sum total of the data thus far brought to light makes the basis for this observation abundantly clear. With regard to earlier times, our knowledge is far more fragmentary and elusive, and the evidence is very much more difficult to interpret. Within certain limits, however, R. B. Dixon's (1928, p. 31) statement that "the extent of the dependence of culture on environment and the closeness of correlation between them is greatest in the lower stages of cultural growth" seems to apply. Thus prehistoric archaeology cannot be divorced from its background of the natural sciences without denying it the very key to the solution of its fundamental problem: the reconstruction and interpretation, insofar as possible, of human activities of the past. Few prehistoric archaeologists today would disagree with this concept; but it was not appreciated by most early workers in the field, who seem to have felt that, in producing an orderly classification and description of their material, and comparing it superficially with analogous collections from elsewhere in the region, their job was done. It is the direct result of the shortcomings of this purely formal taxonomic approach which has in large measure abstracted the data from their real context, and which is the underlying cause of the dilemma in which prehistoric archaeology finds itself today.

Scope and Relation to the Natural Sciences

Prehistoric archaeology in the Old World is so basically and fundamentally dependent on the natural sciences that the dividing line between them cannot be clearly defined. Thus man himself is both a natural and a social being. On the natural side he belongs to the animal kingdom; phylogenetically he has, along with the higher apes, inherited certain physical attributes from a common paleoanthropoidal ancestral stock. But no one can deny that the degree of morphological divergence between living men and apes is tremendous. One basic reason for this divergence has been the capacity of the human organism to develop a material culture—to invent a varied assortment of implements to assist him in his struggle for survival. The archaeological record demonstrates that it has been mainly because of his progressive ability to devise new types of tools, as well as techniques for their manufacture, that man has finally been able to emerge as the only mammal which today has become almost entirely liberated from the limiting factors imposed by environmental and geographical conditions. It is, therefore, the direct result of his ability to apply common sense and reason to the solution of a given problem and, once having arrived at this solution, to be able to impart the knowledge and experience thus gained to others of his kind, which sets off the study of early man in a realm apart from the disciplines governing the natural sciences. In other words, the fact that, somewhere at a very early hominid or pre-hominid level, man acquired an ability to apply reason to his daily problems is considered of paramount importance in the development of human culture, both past and present.

The extent to which social factors have influenced indirectly the physical development of man[2] is a problem almost impossible of solution

[2] Probably the development of tools played an important, if not a decisive, role in the reduction in the size of the jaw, which in turn seems to have resulted in a general enlargement of the brain, by making possible an expansion in the size of the brain case. This expansion has been denied the higher Primates, owing, apparently, to the

Indeed it seems very unlikely that any anthropologist will ever be able to offer anything more specific than a plausible answer to it. Furthermore, we know very little as yet concerning the actual influence of invironment on the physical development of the human organism. In that new mutations must have been constantly produced in response to the profound changes in climatic conditions, the rhythmic nature of whose recurrence characterizes the entire Pleistocene epoch, the biologic selection of forms better adapted to a given set of new conditions must have played an important part in the splitting up of the human family into the complex racial pattern found in the world at present. With regard to the development of early human cultures, however, prehistoric archaeologists are becoming more and more convinced that environmental factors in the broad sense exerted a profound influence. Here an approach developed by ethnology can be applied, although between the two closely related disciplines there are several important and basic distinctions. First, in most instances, the prehistoric archaeologist is able to recover only those objects of man's handiwork which have withstood the ravages of time. He is, therefore, considerably limited in regard to the data available to him with which he must attempt a reconstruction of the material culture of a given group. Secondly, the work of the ethnologist concerns the activities of people existing at present in those parts of the world for which we have no consecutive historical records; whereas the prehistoric archaeologist is constantly faced with the question of time—*i.e.*, chronology—a factor of the first order of importance. The obvious approach to the latter problem is through the fields of geology and those closely allied sciences that deal with the deposits of late Cenozoic time, especially vertebrate paleontology and paleobotany. In that a firmly established chronology for a given region must rest on a foundation constructed of a synthesis which considers the sum total of the available data, the environmental background, fundamental to a reasonably accurate interpretation and evaluation of the prehistoric archaeological material, will inevitably emerge. On this basis, the close degree of interplay between prehistoric archaeology (or paleoethnology) and the natural sciences at once becomes apparent.

The following is offered as a possible definition of the dividing line between prehistoric archaeology and the natural sciences:

> Prehistoric archaeology may be regarded as ethnology projected backward in time until it is forced into intimate contact with the natural sciences, on which it must rely entirely both for chronological purposes and for establishing the environmental conditions that obtained during the particular stage of the Pleistocene under consideration.

The rigid taxonomic laws governing the natural sciences do not apply in prehistoric archaeology, since the tools themselves are direct material manifestations of thinking. In other words, they are documents of human experience. For this reason, the imperishable products of the material cultures of the men of the Old Stone Age must always be considered as *social* rather than as *natural* phenomena.

The significance of the newer approach to the study of prehistoric cultures has recently been fully discussed by Childe (1948, p. 51), who states

> "artifacts hang together in assemblages that recur repeatedly, not only because they were used in the same 'age', but also because they were used by the same people, made or executed in accordance with techniques, rites or styles prescribed by a social tradition, handed on by precept and example, not by biological means, and modifiable in the same way."

In this manner, as Childe aptly points out, the prehistoric archaeologist studies not merely relics and monuments, but assemblages of these, which may be recognized as prehistoric cultures.

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stricting effect of the enormous musculature necessary for the proper functioning of a protuberant jaw. With a larger and correspondingly more complex brain (there is, of course, no positive correlation between gross size and intelligence), there would be a potential increase in the capacity of the organism to apply reason and forethought to daily problems. Since the latter factor would tend to increase the ability to originate new techniques or modify and improve old ones, even more subtle physical changes, in addition to a gradual recession of the snout, may well have resulted. In the final analysis, therefore, this process may be regarded as a self-accelerating phenomenon.

These in turn represent societies—distinctively human groups or units—rather than mere collections of lifeless objects.

Notwithstanding the fact that research on Early Man is intimately and directly related to the study of Pleistocene stratigraphy, it must be constantly borne in mind that this relationship with the natural sciences is strictly in the nature of an alliance. Fundamental to the establishment of the age of a given Palaeolithic implement-bearing horizon is a detailed geologic and paleontologic study of the Pleistocene strata in the region. Indeed the contributions of archaeology to the stratigraphic column, in the sense the geologists conceive of the latter, is virtually nil: for the implements themselves, being variable, cannot be used for dating purposes, except within certain broad categories. Furthermore, before a prehistoric culture of established antiquity in one region can be correlated with comparable developments in contiguous regions, some sort of reliable sequence for the several regions under consideration must be worked out. Unfortunately, at the present time such sequences exist only in a very few parts of the Old World. This situation directly reflects the very limited amount of specialized work that has been done along these lines, rather than either a lack of pertinent data or a dearth of regions that lend themselves to this approach.

Limitations of Prehistoric Archaeology

In general the Palaeolithic, or Old Stone Age, has been thought of in terms of a succession of types of flint implements, named from various sites in France, which, although admittedly produced by man, were sufficiently constant to permit their use as "zone fossils." Unfortunately for those who would like to turn to prehistoric archaeology for correlation studies, research during the last 25 years has shown that this is emphatically *not* true. Although its techniques for classifying and comparing the concrete physical objects with which it deals suggest a superficial relationship between prehistoric archaeology and paleontology, the nature of the basic problems involved and the methods of research employed closely ally it with ethnology, a branch of history, which in turn is one of the humanistic disciplines. Since it differs from ethnology in that the time factor is ever present, paleoethnology is perhaps a better term to propose as a synonym.

The fundamental difficulty, which is an ever-present factor in prehistoric archaeology, is the incompleteness of the record. This is particularly true of the early stages of man's cultural development, the factual documentation on which is extremely meager. This makes it virtually impossible at present to define *culture areas*, or even the *regional distribution* of the multitude of extinct Stone Age cultures reported from various parts of the Old World, each of which must have been a complete and functioning whole at a given stage of the Pleistocene. Only through a full understanding of the time dimension are we ever going to be able to establish the interrelations of these cultures. When added to this we have their spatial arrangement, it may be appreciated how extremely complex the total picture ultimately may prove to be. Furthermore, since only a small percentage of the data have been preserved, the paleoethnologist is forced to restrict his interpretations in the main to the more material aspects of a given prehistoric culture. Indeed in many instances, especially for the early periods, the archaeological facts are

> "so few and fragmentary that we are almost obliged to fill them up and connect them by subjective speculative interpretations. These may easily turn into metaphysics, into hypotheses, that cannot possibly be tested by experience and controlled by observation." (Childe, 1944a, p. 7.)

However, since most prehistorians are now fairly well aware of the shortcomings of the taxonomic approach to their subject, the danger of prehistory degenerating into metaphysics is certainly more remote today than it was a decade ago, although it is by no means non-existent. But there is a growing consciousness that a reconstruction of the pattern of events that occurred during Stone Age times can only be achieved by archaeology as one of a combination of sciences, in which the controlling position clearly belongs to geology. In the final analysis, the geologists will have to date the various cultural horizons in a given region for the archaeologist, rather than vice versa.

Research in the field of Stone Age archaeology

during recent years has led to general recognition of the fact that the archaeologist must accept the conclusions of the geologist. If the work is professionally done, he certainly should not adopt the attitude that he is qualified to pass judgment on these conclusions. Having ascertained the age of a given horizon from the geologist, the archaeologist should proceed from there with the interpretation of his material. The real trouble is that in many instances the archaeologist himself has been compelled to try to establish the geologic succession, an undertaking for which he is normally ill-equipped because his training throughout has emphasized the humanistic nature of the discipline he purports to represent. The results are almost equally deplorable if a geologist attempts to work out and interpret the archaeological sequence of a given region. The time has come for the natural scientists to realize that, in attempting to use any given type of stone artifact in correlation studies, the prehistoric archaeologist is at a complete loss (whether he admits it or not), mainly because the vertical ranges of the various classes of tools are unknown. Moreover, in any single instance a selected group of artifacts may well represent the survival of an ancient tool-making tradition. Therefore, we must rely on an overall picture of the cultural assemblage from any specific horizon, but in the first instance a knowledge of the stratigraphic position of the deposits, as determined by the geologic and paleontologic evidence, is a prerequisite, if we expect to achieve anything more than a pure taxonomic study.

The hopes once entertained by geologists that archaeology would provide them with factual evidence for establishing correlations have recently received several setbacks. This situation directly reflects the growing realization that the Palaeolithic cultural succession in any given region, with its many local variations, is infinitely more complex than was appreciated by the early workers. As an example, the case of Baker's Hole, Northfleet, in the Thames Valley (Oakley, 1943, p. 31; Oakley and King, 1945; Breuil, 1947) may be cited. Originally the implements from beneath the Coombe Rock at Baker's Hole were identified as Early Levallois (I–II) in terms of Breuil's sequence in the Somme Valley. On this basis the Coombe Rock is the equivalent of the "Great Eastern glaciation," Stage X of the sequence worked out by King and Oakley in 1936, and presumably the British counterpart of the Riss Glaciation of the Alps. From point of view of the Thames succession as a whole, this correlation seems to "fit" very well with the observed facts, and it was believed to provide a sound tie-in with the Pleistocene sequence of the continent. It has now been found, however, that bifacial hand-axes of evolved Acheulian type occur in direct association with the industry in question, which would make it the equivalent of Late Levallois (V) by analogy with the Somme succession. If this is the case, the associated deposit of Coombe Rock may have to be transferred from the Third (Riss) to the early Fourth (Würm I) Glacial stage. On the other hand, Acheul-Levallois contact may have taken place in Southern Britain earlier than in Northern France, but such a likelihood seems extremely improbable in view of the proximity of the two regions.

As a further example of why geologists are beginning to distrust the use of aechaeological evidence, one may mention the very fundamental problem of the interrelations of core (Abbevillian, Acheulian) and flake (Clactonian, Levalloisian, Tayacian, Mousterian) tool traditions recently reviewed by R. J. Braidwood (1946, p. 145–152). Both traditions are known to occur as early as the First (Günz-Mindel) Interglacial stage and to have persisted into Fourth Glacial times. The problem is very complex and confusing. Formerly it was thought that the core (or bifacial) tools were most typical of beds assigned to warm interglacial times, whereas the flake (or unifacial) tools seemed to be normally associated with beds concomitant with stages of glaciation. (*Compare* for instance Bailly, 1939.) It has further been suggested that the two different traditions belonged to two distinct groups of population—the flake tools to men of Paleoanthropic type and the core tools to Neanthropic man. The recent finding of Neanthropic (*H. sapiens*) remains at the Cave of Fontéchevade (Charente), in Central France, in a horizon that yielded a Tayacian (flake-tool) industry pretty

well vitiates this theory (Henri-Martin, 1946; 1947; Vallois, 1947; Movius, 1948; Eiseley, 1948a). In addition, recognition of the fact that flake tools likewise occur directly associated with *all* of the so-called biface cultures (Kelley, 1937) has tended to make most workers suspicious of the very existence of any clear-cut basis for differentiating between the two traditions. Not only do Clacton-type flakes manufactured by the primitive block-on-block technique occur in northwest Africa in deposits containing rough bifaces (Neuville and Ruhlman, 1941), but also flake implements made by the well-known Levallois (faceted platform) technique are apparently typical throughout most of those regions of the Old World where biface complexes of developed Acheulian type are found, although this is apparently not true of the sites in Western Europe (Movius, 1944). On the basis of present evidence, this last-named area, on the extreme northwestern periphery of the distribution of biface cultures, is one of the few regions where core tools of the Acheulian complex and the flake industries of the Levallois tradition can be segregated. Elsewhere, with the possible exception of Palestine (*cf.* Garrod and Bate, 1937, p. 78–89), these two appear to be mutually related, a situation apparently true throughout Africa (Van Riet Lowe, 1944; 1945) and in Peninsular India, as far as can be determined. In Egypt, a centrally located region, hand-axes of Upper Acheulian type occur in direct association with flakes manufactured by the classic Levallois technique (Huzayyin, 1941, p. 174–194; Caton-Thompson, 1946a). In discussing Lower Palaeolithic techniques employed in the Belgian Congo, C. van Riet Lowe (1944, p. 170) states that there is

> "no vertical division between the essential flake and core techniques in the Congo as there apparently is in Western Europe. The situation is precisely the same throughout Africa from the basin of the Nile to the Cape of Good Hope."

Both J. Desmond Clark (1939) and Neville Jones (1938) have arrived at substantially the same conclusion on the basis of quite independent evidence from Northern and Southern Rhodesia.

The above summary of the core *vs* flake-tool tradition problem demonstrates not only that there is no general measure of agreement among archaeologists as regards the significance of this material, but also that the approach of the prehistorian to the problems with which he deals is fundamentally different from that of the professionally trained natural scientist. In other words, a stone tool of a certain type is a human and *not* a natural product; it can never have the same stratigraphic significance as, for instance, a lower molar of *Loxodonta* (*Hesperoloxodon*) *antiquus*, a glacially striated boulder, or an ancient soil that has been altered by chemical weathering. Furthermore, since recent work in Portugal has shown that industries basically of Mousterian tradition persisted there through *all* substages of the last glacial stage (Breuil and Zbyszewski, 1942; Zbyszewski, 1943), one begins to doubt the validity of the old divisions of Lower, Middle, and Upper Palaeolithic, even when these are brought into line with the new axis of so-called core, flake, and blade traditions. Indeed, on the basis of the typology of the stone tools, one would assess the demonstrably Middle Pleistocene fissure deposit at Choukoutien: Locality 1, which has yielded the rich *Sinanthropus* material, as early Lower Pleistocene by analogy with comparable material from South and East Africa.

Conclusions

During the last 25 years prehistoric archaeology has made rapid strides. It has advanced to the point at which it now recognizes that humanity in the past, like humanity in the present, was complex. But we do not yet understand the full implications of these complexities, among which there must inevitably exist a number of distinctive unities. Most prehistorians today, however, are fully aware of the essential truth of the statement that *we can no longer deal in the abstract with humanity*. As previously stated, prehistoric archaeology is a social science, a specialized subdivision of cultural anthropology, and the objects with which it deals must always be regarded as the imperishable products of man's manufacture—tools designed to assist him in his struggle for survival; "to ignore this element of incalculability is to force prehistory into a strait-jacket" (Garrod, 1946, p. 9). To the writer

the soundest approach to the study of a series of tools from a given horizon seems to be through the natural sciences which are concerned with the sequence and correlation of events during the Pleistocene—geologic, climatic, and biologic. Since they alone are capable of introducing the all-important and closely interwoven time and environmental factors, the essential interest of prehistoric archaeologists in them may be summarized as follows: (1) for the establishment of a relative time scale by means of which the fossil remains of early man and his cultural relics may be placed in their proper sequence; (2) for the study of developing technology and material culture, as well as the survival(s) of ancient tool-making habits or traditions; and (3) for the reconstruction of the changing environmental (biogeographical *or* ecological) conditions which confronted man during the Pleistocene in his effort to gain dominance over the forces supplied by nature. In essence it is man's progressive ability to cope with the forces of nature that prehistorians are studying. Therefore, if the environmental factors played the dominant role in modifying the material culture of our Stone Age ancestors, an understanding of these factors should ultimately provide the key to interpreting the paleoethnological significance and relationships (if any) of the changing food-gathering culture patterns found throughout the Old World during the Pleistocene epoch. In this sense the several fields under discussion are closely allied.

With regard to (2) above, the study of the traits constituting the material cultures that existed during prehistoric times is essentially a study of inventions and discoveries, as well as the subsequent diffusion of these new techniques of manufacturing tools and new types of artifacts, or combinations of both, which further emphasizes the fact that prehistorians are completely dependent on those sciences that deal with dating and stratigraphy. At present the vertical ranges and regional variations of the various tool-making techniques and implement types of the Stone Age are virtually unknown, except within limits far too broad to be of any use as stratigraphic indicators. And very probably this situation will prevail for many years to come. In any case, prehistoric archaeology today can offer very little to the natural sciences concerned with Pleistocene research, except in a broad sense, beyond the fact that it provides an intensely interesting and stimulating point on which to focus stratigraphic and correlation studies. For, with the unravelling of man's past civilizations as the primary objective, the several fields that cover Pleistocene studies receive a fresh impetus.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

8. SUBMARINE GEOLOGY AND PLEISTOCENE RESEARCH

By Fred B Phleger

The upper layers of marine sediments hold the key to the Pleistocene (including postglacial) history of the ocean basins, and this can be obtained through the collection and study of long submarine cores. Before the sequence of sedimentary events recorded in these cores can be interpreted we must have an accurate knowledge of the relationship between the sediments now being deposited and their various environments. There is relatively little accurate information on the environmental factors of marine sedimentation, although some of the broader aspects are fairly well understood. Any marine deposit is conditioned by all the features of the environment and cannot be considered as separate from the water above and around it. It is necessary, therefore, to understand all the physical, chemical, and biological aspects of an ocean for a proper understanding of a sediment. Our knowledge of marine environments progresses slowly because of the size of the ocean and the difficulty and expense of study.

A marine sediment may be considered to be composed of two types of materials: (1) inorganic particles of sand, silt, clay, or chemical precipitates; and (2) organic remains, composed of skeletons of organisms, organic carbohydrates, and undifferentiated organic debris. The marine environment conditions the grain size, grain-size distribution, certain inorganic chemical features, and the mass physical properties of a sediment. The environment also determines the nature of the recognizable skeletal organic remains in any marine sediment, since plants and animals have more or less specific adaptations to temperature, salinity, nutrient supply, and other factors. Recognizable skeletons in sediments are the most useful tools in deciphering an environment in which a marine sediment was deposited. The organisms most useful in this respect are the Foraminifera because they occur in all marine and brackish-water sediments and also because of their small size and great abundance. Radiolaria, diatoms, ostracods, and other forms might be used, but generally these are more difficult to work with. It is on the basis of environments indicated by the vertical distribution of Foraminifera faunas that the Pleistocene age of parts of some of the submarine cores collected from areas in the Atlantic, Pacific, and Mediterranean has been suggested.

Foraminifera are both planktonic and benthonic. In deep-sea deposits (2000 meters or more) over 99 per cent of the Foraminifera tests belong to planktonic species, and it is in deep-sea cores that vertical faunal differences have been most common. Recent evidence indicates that the planktonic species may live in abundance throughout a great range in depth—2000 meters or more. Thus any fauna of planktonic Foraminifera may have been conditioned by the entire vertical temperature structure of the water.

Modern Foraminifera assemblages, both planktonic and benthonic, differ in different oceanic areas. A study of the distributional features shows a good correlation between faunas and surface and bottom water temperatures. Other factors also are important, principally salinity and the type of sediment, but it is possible to segregate these ecologic factors from the temperature effect. Hutchins (1947) has analyzed the effect of temperature ranges

on *Balanus balanoides* and other marine organisms based on distribution data of the organisms and correlated with physiological studies. There is no reasonable doubt that Foraminifera populations have temperature adaptations comparable to those demonstrated by Hutchins.

In most of the long cores studied from deep water in middle and low latitudes there is a fauna at some distance beneath the sea floor which was deposited during a time of colder-water conditions than those now obtaining. In the tropical areas of the South Atlantic (Schott, 1935) this colder-water fauna is characterized by the absence of one abundant tropical species. In the Gulf of Mexico (Phleger unpublished) and on the continental slope and basin of the western North Atlantic (Phleger, 1939; 1942) in middle latitudes the cold-water fauna is subarctic or cool-temperate. In the Caribbean the "cold-water" fauna is warm-temperate or cool-temperate (Cushman, 1941; Phleger, 1948). In a few cores from the North Atlantic more than one cold-water fauna is separated by one or more warm-water faunas (Cushman and Henbest, 1940; Phleger and Hamilton, 1946). These colder-water faunas are interpreted as Pleistocene in age, certainly last glacial, and possibly as representing substages of the last glacial. Three long cores from the Tyrrhenian Sea (Phleger, 1947), and cores from the Arabian Sea (Stubbings, 1939), show similar faunal variations.

A reconnaissance study by the author has been made of the Foraminifera faunas of a core 15.4 meters from a depth of 2600 fathoms in the Caribbean Sea. At least 11, and probably 12, shifts from tropical to temperate conditions are indicated by the vertical distribution of the faunas. A thick tropical fauna near the mid-section of the core is suggested as possibly representing the Second Interglacial; further, the core may have penetrated most of the Pleistocene. This core suggests the possibility of glacial substages in the third and second, and possibly the first, glacial stages.

The recognition of these probable glacial stages and/or substages in submarine cores is based on the relationships among the faunas which occur in vertical sequence in any core. The top core fauna is taken as the one representing modern conditions obtaining where the core was collected. Faunas beneath the top one are determined as representing the same or different temperature conditions from the present ones at that place. The species of Foraminifera in these lower faunas are all living at the present time; no submarine core fauna examined by the writer and his colleagues has contained any extinct species. The probable relative surface-water temperatures are determined in a general way, by a comparison of the sequence of core faunas with what is now known of the distribution of modern Foraminifera. Planktonic species are used in this analysis almost exclusively. It is not possible, at the present state of our knowledge, to indicate the actual temperatures indicated by these lower core faunas. One possible exception is in studies now in progress on cores from the Gulf of Mexico: The lower core faunas, late glacial in age, probably were adapted to water temperatures similar to those now obtaining above the continental slope north of Cape Hatteras. This surface-water areas has a yearly maximum temperature about 5° F. less and a minimum temperature about 20° F. less than the present temperatures in the Gulf of Mexico.

Continued study of the vertical faunal variations in submarine cores eventually should make it possible to reconstruct the late Pleistocene history of the oceans. It will be necessary to accumulate more useable information on the ecology of Foraminifera, but some progress is being made in this direction. It should be possible, eventually, to reconstruct for the entire ocean the marine temperature conditions which obtained during a part of the Pleistocene. This knowledge should have an important bearing upon our understanding of the sequence of climatic events on adjacent lands. Such information may be of great value in determining the Pleistocene climates in certain areas which were land bridges for the migration of land vertebrates. According to Claude W. Hibbard (personal communication):

> "Very little is known in regard to the land-bridge via Central America. We know that there has been an exchange of vertebrates over this bridge between South America and North America. There has been considerable speculation about the change of temperature and climate in the Central American region to provide corridors which at present do not exist but should have existed in the past to allow the movement of forms."

The collection and study of cores from approproate marine areas adjacent to Central America should aid in solving this problem.

It is of interest to speculate on the probable general distribution of water temperatures in the ocean during a glacial stage of the Pleistocene. Studies indicate that there was general cooling of the water in middle and low latitudes. This is seen in cores collected in the Gulf of Mexico, low latitudes of the South Atlantic, the Arabian Sea, and the Caribbean, and in middle latitudes of the North Atlantic and Mediterranean. The amount of cooling in degrees would be expected to vary from place to place and may reach as much as 10° F. for summer maximum and perhaps more for winter minimum temperatures. It appears doubtful whether truly Arctic and Antarctic waters were appreciably cooled since these regions now have temperatures which are at an approximate minimum to be expected under any conditions.

The broad features of oceanic circulation would probably be similar to the present circulation, with two important exceptions. The clockwise and counter-clockwise circulation which brings tropical water into high latitudes probably was telescoped into lower latitudes. This would be effected by the greatly enlarged masses of Arctic and Antarctic water acting as a density barrier to the distribution of the warm water as far poleward as at the present time. Ice-rafted pebbles have been collected by Henry C. Stetson and the writer in one submarine core from the western North Atlantic as far south as approximately 40° N. Lat. These probably were deposited by icebergs, and it is to be presumed that the cold Arctic water extended somewhat south of this latitude; quite possibly pack ice extended as far south as 40° N. Lat. Under these circumstances the Gulf Stream system of the North Atlantic undoubtedly would be barred from carrying relatively warm surface water near the European continent, and similar conditions are to be expected in other similar current systems. It is doubtful whether the northern edge of the Gulf Stream system reached a latitude much higher than that of Cape Hatteras on the North American continent.

Lowered sea level during a glacial age and the deflection of the current systems by the masses of cold water would present a series of topographic barriers to oceanic circulation. The main features of this circulation can be reconstructed for the last glacial age on the basis of information already available. There is a further possibility, however, which promises more reliable results. Water masses can be identified by their assemblages of planktonic Foraminifera. There should be no great difficulty in tracing the distribution of water masses for the various stages of the Pleistocene when sufficient core material has become available. This will involve careful correlation of the relatively cold-water lower faunas in the cores, but such correlation is somewhat simplified by the preservation of the complete record in the deep sea. The positions at which deep-sea cores are collected should be determined on the basis of these possibilities.

Another important contribution of this research is the possibility it offers of correlating the North American Pleistocene with that of Europe. This can be aided by the use of pollen as a tie-in from land to sea where a submarine Pleistocene Foraminifera fauna occurs near land. In the Gulf of Maine such a fauna is widespread in short cores taken within 15 miles miles of land. This appears to be an ideal location to make a tie-in between North America and the submarine sequence. A similar tie-in should be possible between the marine sequence and the European glacial sequence in places such as the North Sea.

It appears that the only environment in which an undisturbed record of the complete Pleistocene is preserved is in the ocean basins. It may even be desirable to establish a "type section" for the Pleistocene based upon long cores of deep-sea sediments. The best region for such a purpose is perhaps the Mediterranean where it may be possible to correlate the results with the Pleistocene sequence in the Alps and also with the excellent sequence of prehistoric man in that region (Bradley, 1938). A series of long submarine cores recently have been collected from the Mediterranean by members of Oceanografiska Institutet of Göteborg. Study of these cores will be begun during the summer of 1949 by members of the Marine Foraminifera Laboratory.

There is little published information on conditions of sedimentation in offshore marine areas during the Pleistocene. Daly (1936) and

others have suggested that lowered sea level during a glacial age would expose great areas of mud on the lower part of continental shelves. Wave action on these exposed shelves would put great quantities of fine-grained sediments into suspension. Most of these materials would be deposited on the continental slopes, but some might reach the ocean basins. A relatively thick deposit of fine-grained sediments would accumulate, at least on the slope areas, during a glacial age or subage. In addition, because of lowered sea level, the rivers would be expected to carry greater quantities of sediment into the ocean than at present due to an increase of gradient, at least in the lower parts of river courses.

The sediment containing late-glacial Foraminifera faunas is generally thicker than that containing postglacial faunas on the continental slope areas studied. This is not necessarily true in the sediments collected from the ocean basins far from large land masses, as in the Caribbean. In the Gulf of Mexico, a relatively enclosed basin adjacent to large land areas, sedimentation was rapid in places at great depth during the last glacial age (or subage). Cross-bedded sand was deposited in parts of the Sigsbee Deep at this time (Trask, *et al.*, 1947). Evidence of rapid sedimentation during glacial times is seen in the Tyrrhenian Sea and also in a deep basin adjacent to a large land area (Phleger, 1947).

Large amounts of fine-grained sediment in sediment in suspension would make ocean water much more turbid than at present over large areas of the world. This turbidity would limit the depth of light penetration and thus the depth of effective photosynthesis. The production of marine plankton and all other organisms would be reduced under such conconditions. The writer has observed that Foraminifera populations usually are much smaller in late-glacial than in postglacial marine sediments. It is believed that this is due in part to lower organic production. These apparently lower populations undoubtedly are accentuated by a more rapid rate of deposition of inorganic materials.

Submarine coring devices in use until recently could obtain cores rarely more than 10 feet in length, although one has been reported 17 feet long. Kullenberg (1947) has adapted a piston core sampler which obtains undisturbed cores 20 meters in length in certain types of materials. Use of this instrument will greatly add to our knowledge of oceanic history. The Swedish Deep Sea Expedition recently completed a round-the-world cruise principally to take cores with the Kullenberg sampler. This expedition obtained approximately 200 long cores from all the major ocean basins in low latitudes. This material and the cores being collected by other organizations in this country should provide invaluable data.

The study of the Pleistocene history of the ocean is an infant science, and the present accomplishments are not great. Collection of material from the ocean is expensive, and the subsequent study and interpretation are laborious and specialized. The principal techniques of field work and laboratory study are now established. It is believed that considerable progress will be made in the next few years in determining the sequence of marine events and environments during glacial and interglacial times. This information will aid in analyzing the Pleistocene history of the continents and in understanding the sequence and distribution of environments for the Earth as a whole.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

9. PROBLEMS OF PLEISTOCENE STRATIGRAPHY

By Louis L. Ray

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Introduction

History of the present and of the recent past is difficult to analyze because the wealth of detailed information available commonly conceals the major issues by its kaleidoscopic patterns. However, when viewed in retrospect, after a long period of time, details of the intricate patterns are lost, and there emerges a simple and clearly defined picture of the major trends. So it is with the Pleistocene. Every landscape bears a wealth of detailed information so complex, so varied, and generally so localized that it is difficult to recognize the major pattern into which the data can be placed. Essentially the problems of Pleistocene stratigraphy are similar to those of earlier geologic times, yet in detail the techniques and methods used in solving the stratigraphic problems differ widely. Many cannot be solved by the geologist alone, but require the co-ordinated efforts of specialists in widely divergent fields.

The final solution of the many problems and the establishment of a Pleistocene stratigraphy are only a means to an end—the chronology of events which have led to the physical conditions of the present. An attempt is here made to indicate the complexities of the problems, the need for correlation among many fields of science, and the present status of Pleistocene stratigraphy.

Terminology of Pleistocene Stratigraphy

The Pleistocene Epoch

The first problem in the stratigraphy of the Pleistocene is the definition of the term and the establishment of the limits of the time to which it applies. Despite the fact that the term Pleistocene was introduced by Lyell in 1839 and applied to strata whose content of fossil mollusks included more than 70 per cent of living species, this problem of definition is as yet unsolved.

General usage in the United States considers the Pleistocene (or "Glacial") to be the first epoch of the Quaternary period; the Recent, which extends to the present, is the second epoch.[1] The important boundary between the Pliocene and Pleistocene epochs, which also marks the division between the Tertiary and Quaternary periods of the Cenozoic era, has never been adequately defined, for it is transitional, unmarked by any large unconformity or

[1] Usage adopted by the U. S. Geological Survey; *see* Wilmarth (1925).

changes in fauna or flora, in contrast to other divisions of similar value in the stratigraphic column. The general belief has recently been stated that the major distinction between the Pliocene and Pleistocene is one of climatic change. Flint (1948) has discussed this problem in considerable detail and supports the belief that the Pleistocene is "that part of late-Cenozoic time which is characterized by repeated climatic cooling. . . ." These climatic fluctuations have produced world-wide effects which are assigned to the Pleistocene. The fluctuations produced repeated glaciations in high latitudes and high altitudes, together with a host of attendant but less spectacular changes elsewhere. They can be observed in the fauna, flora, soils, isostatic readjustments of the land, eustatic changes of sea level, and in the geomorphic development of the landscape, but are often difficult to recognize in regions remote from glaciers. Synchronous with the Pleistocene has been the development of man, whose artifacts and skeletal remains were hailed as important stratigraphic horizon markers. Recent studies, however, throw doubt on the amount of definite aid that can be derived from archaeological research.

The troublesome lower boundary of the Pleistocene has never been adequately defined, despite many attempts. (*See* such recent studies as Pilgrim, 1944, and Zeuner, 1945). At the Eighteenth Session of the International Geological Congress (London, 1948), a Temporary Commission on the Pliocene-Pleistocene Boundary was appointed, and numerous papers read dealt with the problem of defining this boundary. This Commission reported,

> "that this boundary should be based on changes in marine faunas, since this is the classic method of grouping fossiliferous strata. The classic area of marine sedimentation in Italy is regarded as the area where this principle can be best implemented. It is here too that terrestrial equivalents of the marine faunas under consideration can be determined." The Commission recommended, "that, in order to eliminate existing ambiguities, the term Lower Pleistocene should include as its basal member in the type area the Calabrian formation (Marine) together with its terrestrial equivalent the Villafranchian."

It was

> "noted that according to evidence given this usage would place the boundary at the horizon of the first indications of climatic deterioration in the Italian Neogene succession" (King and Oakley, 1949; Oakley, 1949).

The upper boundary, marking the close of the Pleistocene epoch and beginning of the Recent epoch, has been established in a variety of ways by many workers, but none has proved satisfactory (Antevs, 1931; De Geer, 1912; Leverett and Taylor, 1915; Morgan, 1926; Russell, 1940, and others). All are arbitrary, and, while some may be locally useful, none has world-wide application.

To many, the Pleistocene epoch is the equivalent of the *glacial*, the Recent epoch the equivalent of *postglacial*. In glaciated regions such a distinction is valid when used locally, but, as all areas were not freed of ice simultaneously, the use of these terms in a regional sense is not justified. Furthermore, in areas remote from glaciers, where there are no effects directly referable to them, the terms are inapplicable. Thus, the upper limit of the Pleistocene epoch, defined in a variety of ways, lacks real validity on the basis of any field evidence yet proposed.

Flint (1948) has suggested that, since there is no recognizable division but only a transition between the Pleistocene and Recent epochs, Recent be dropped and Pleistocene be extended to encompass all of post-Pliocene time, the terms recent and postglacial being used only in an informal sense. This modification of the geologic classification will be welcomed by many geologists who believe, because of the lack of a definite break in the stratigraphic sequence and because of our existing glaciers and a present-day climate cooler than one of the interglacial ages of the undisputed Pleistocene, that we are still in the Pleistocene epoch. Although this important problem of classification needs much further study by specialists in the many fields of science dealing with this period of earth history, it is adopted and used in this report because of its simplicity and convenience. The reader is referred to a review of the subject by Flint (1948, p. 197–209).

Subdivisions of the Pleistocene Epoch

As the concept of widespread climatic fluctuations is basic in determining the boundaries of the Pleistocene epoch, so are the results of the

climatic fluctuations basic in determining the subdivisions of this epoch.

The most obvious results of the climatic fluctuations were the generation of widespread glaciers during climatic cold periods, and the dissipation, perhaps almost total extinction, of glaciers during climatic warm periods. Major alternations of ice advance and recession, recognized long ago through the classic studies of Chamberlin and Salisbury in North America, and of Penck and Brückner in the Alps, provide the best-known sequence of Pleistocene events and form the basis for an absolute climatic chronology, to which the stratigraphic sequence can be correlated. To clarify the terminology applicable to these major divisions of the Pleistocene, making it conformable with the most generally accepted usage, it has been proposed (Flint, 1942; Flint and Moore, 1948) that glacial and interglacial times should be termed *ages*, and that their stratigraphic equivalents be termed *stages*. Such standardization of terminology with a careful distinction in the use of time and time-rock terms will aid greatly in the clarification of the confusion developed in the voluminous Pleistocene literature, especially in studies of nonglaciated regions.

Little information is available concerning minor fluctuations within any but the last glacial age, which has been shown to consist of several minor advances and recessions. Following the suggested terminology distinguishing between time and time-rock terms, these minor episodes become *subages* and their stratigraphic equivalents *substages*.

Indirectly, the basis for all Pleistocene stratigraphy rests on *climatic changes* whose ultimate cause is as yet not known. As the wealth of information accumulates concerning the major and minor world-wide advances and recessions of glaciers, it is more and more apparent that the climatic fluctuations were world-wide and broadly synchronous. Without this assurance, attempts at world-wide correlation of the Pleistocene would be almost impossible.

Status and Problems of Pleistocene Stratigraphy

General Status

In glaciated regions, sequences of glacial deposits can readily be correlated with past climatic events, and a local chronology can be established suitable for incorporation into the major world-wide sequence of events. In nonglaciated areas, the problem of establishing a local sequence of climatic events and of correlation with the world-wide chronology is more difficult; the difficulties increase with distance from glaciated areas. Adjacent to the glaciated areas is a belt of indefinite width, commonly referred to as the periglacial zone, in which the effects of climatic refrigeration can be directly associated with the glaciation and thereby fitted into the world-wide sequence of events. In areas remote from the glaciated regions, where there are no effects directly correlative with the ice masses and where climatic fluctuations have been less intense, stratigraphic correlation becomes increasingly difficult and in many cases impossible with the present state of knowledge. In these areas the combined efforts of many specialists are needed to solve the problems of stratigraphy.

Workers have recognized Pleistocene sequences of events in many widely separated localities. Such studies as those of Caldenius (1932) in Patagonia and Tierra del Fuego, Nilsson (1931; 1935; 1938; 1940) in Africa, De Terra and Paterson (1939) in India, De Terra (1941) in China, Woodring and others (1940; 1943; 1946) in California, and Judson (1946) in the Aleutian Islands have postulated sequences of events by using a variety of data, all of which indicate climatic fluctuations. Numerous attempts have been made to correlate these sequences over wide areas (De Terra, 1941; Nilsson, 1941; 1947) or to review the present status of available data and correlations, and to point out problems for future research (Flint, 1942; 1948; Zeuner, 1945). Within the United States, the need for review and systematic analysis of the Pleistocene data and problems to show the present status of knowledge, and the need for co-operation of workers approaching the problems from many different angles, is shown by recent summary papers (Frye, 1945; 1946; Condra, Reed, and Gordon, 1947; Colbert and others, 1948).

In general four areas can be recognized in which the problems of Pleistocene stratigraphy differ and in which different techniques must be used to place each stratigraphic unit in its

proper position in the sequence of events leading from the first indication of climatic deterioration which marked the close of the Pliocene epoch. These areas are: (1) those of marked climatic fluctuations which have been subject to glaciation, (2) those of indeterminate boundary peripheral to glaciers (periglacial) in which the identifying phenomena are directly related to the glaciers and the glacially modified climate, (3) those areas remote from and only indirectly associated with glaciation through less well marked features indicative of climatic fluctuations, and (4) the little-known submarine areas.

Stratigraphy in Glaciated Areas

The most spectacular evidence of Pleistocene climatic fluctuations is that of multiple continental glaciation, demonstrated by successions of deposits of glacial and interglacial origin. In North America, following the establishment of the concept of multiple glaciation by Chamberlin and Salisbury, the glacial history has been elaborated and refined through the classic monographs of Leverett and the studies of a group of active workers, mainly in the Middle Western States. A sequence of four major glacial ages, separated by interglacial ages as warm or warmer than the present, are recognized. Attempts to subdivide the glacial ages have been directed mainly to the recognition of subages within the last glacial age, where stratigraphic and topographic evidence is best preserved. In Europe, a similar four-fold succession of glacial ages was first recognized by Penck and Brückner in their classic study of the glaciers of the Alps. As in America, the emphasis on subdivision of the glacial ages has been directed to the last glacial age. Summaries in English (Flint, 1948; Movius, 1942; Zeuner, 1945) contain extensive bibliographies of the vast literature on glacial successions, the present status of the knowledge, and intricacies of the Pleistocene stratigraphy.

In a glaciated region it is generally conceded that the Pleistocene opened with the deposition of the first material of glacial origin, although the colder climate which actually marked the beginning of the epoch had been initiated considerably earlier. The length of this time lag between the climatic deterioration and the deposition of glacially derived materials is not known, but must represent a relatively long interval, especially at the terminal positions of the continental ice sheets. As the ice of each successive advance did not cover exactly the same area, either because of differences in magnitude or direction of movement, and as older deposits may have been removed by later advances, only parts of the glaciated areas contain a complete stratigraphic succession of deposits. Insofar as known, the earliest glacial age appears to have been one of the most extensive, giving rise to the speculation that there may have been smaller, preliminary (pre-Nebraskan in North America) ice advances for which no convincing evidence has been found. In Europe, however, evidence for such a series of advances (pre-Günz) has been reported by Eberl (1930) in the Alpine Foreland. Some tentative supporting evidence has been cited in the weathering of the loess in Hungary (Scherf, 1938) and from the periglacial areas of Germany (Zeuner, 1945).

During interglacial ages, glacial deposits of preceding ages or subages were eroded and weathered; erosion surfaces, weathered zones on the glacial deposits (gumbotil), and soil profiles developed. These features indicate the character and, in a general way, the length of interglacial time. Occasionally peat and forest beds contain faunal and floral remains which give a clue to the character of the interglacial climates. Loess deposits, commonly interbedded between glacial deposits of different ages or subages, or marginal to the glaciated areas, can be correlated with the various continental glaciers and form excellent horizon markers because of their wide lateral extent and delicate adjustment to climatic changes through weathering. All these features have been used to distinguish deposits of glacial and interglacial age and subage. The first interglacial age in North America (Aftonian) illustrates the use of these various methods (Holmes, 1942; Lane, 1941) to recognize and reconstruct the interglacial environment and to assign to it an approximate duration of 200,000 years (Kay, 1931).

Frequently deposits of one age can be distinguished from those of others by the lithologic character of the contained rocks (indicator boulders) gathered by ice moving across

different terrains. Similarly, the fabric and size distribution of the till has been used to indicate direction of movement and to differentiate deposits (Holmes, 1941; Hörner, 1944). Only in the most recent age can moraines and similar topographic features be used to indicate extent of a single ice advance. By tracing the deposits and correlating the stratigraphic successions of the widespread continental glaciers, the validity of each glacial age has been established.

Alpine glaciers likewise demonstrate a series of advances and recessions, evidence of which is the sequences of moraines in the valleys, successions of glacial deposits, interglacial periods of valley deepening and cutting, and terraces of outwash material which can be correlated with periods of ice advance. Relations between terraces and moraines can best be established for the subages of the last glaciation and have been used widely in North America (Bryan and Ray, 1940; and others). Where deposits of alpine glaciers are separated from those of continental glaciers, correlation is usually subjective and is based on sequences, depth of weathering, and periods of valley deepening (Antevs, 1945).

Only tentative attempts at correlation between North America and Europe have been made (Antevs, 1928; Bryan and Ray, 1940; Zeuner, 1945), primarily on the basis of similarities in the sequence of events and on the assumption that climatic fluctuations were broadly synchronous throughout the world. In North America it is hoped that continued field studies in areas such as Montana and Alberta, where continental and alpine glacial deposits may have merged, will aid in giving more tangible evidence for correlation. Final world-wide correlation must await validation by reference to a chronology based on climatic fluctuations, in large part substantiated by means of submarine sequences of world-wide extent.

Stratigraphy in Areas Peripheral to Glaciers (Periglacial Zone)

The area adjacent to glaciers, where rigorous climatic conditions prevail, is characterized by a variety of features produced through frost action. Loosely termed the *periglacial zone*, it has been defined by Zeuner (1945, p. 55) as "that zone surrounding an ice-sheet, in which the cooling effect of the ice produced a *frost climate*."[2] Obviously the boundaries are vague and shift with the position of the ice margin. Old periglacial zones can be defined, therefore, only on the basis of the diverse products of a climate in which solifluction layers, polygonboden, block fields, stone rings, stone stripes, involutions in unconsolidated sediments, and related features are developed. However, as these features are the result of a particular climate, great care must be taken in their interpretation, for such features are being produced today in regions far removed from ice masses, where suitable climatic conditions prevail (Butler and Ray, 1946). In regions where such features are not the result of the present climate, as, for example those described by Sharp (1942) in Illinois, they must be assigned to past cold periods. As Zeuner has pointed out, "The periglacial area has furnished by far the most complete evidence of climatic oscillations during the Pleistocene."

The extent of the periglacial zone depends on a multitude of factors such as magnitude and position of the ice mass relative to the regional wind system and to the topography. In general it is conceived to be a zone in which the temperature frequently passed across the freezing point and where winds were probably cold and drying. Since the periglacial climate depends on the ice mass, it fluctuates with the size and position of the ice. Thus, the periglacial zone, in large part, overlaps glaciated areas. However, the outer margin of the zone is the critical area where the so-called periglacial features are unobscured or undestroyed by successive glaciations. Some regions have been within the zone of the periglacial climate more than once during the Pleistocene epoch, each period of frost climate being separated from the previous by a warmer interglacial age or subage. Therefore, when solifluction layers are superimposed one on another, or separated by erosion intervals, weathered zones, loess, or similar features, a stratigraphic succession results

[2] Defined by Zeuner (1945, p. 55) as that climate "where the average temperature is below freezing-point for a large part of the year and where the warmest month averages less than 10°C."

which may be correlative with definite times of ice advance.

Glacial outwash and loess were deposited mainly in the periglacial zone. Successive deposits may commonly be either directly related to definite ice advances or indirectly related through correlation of sequences of events. Interbedded fossiliferous deposits, associated with interglacial ages or subages, have produced a wealth of information on climatic and environmental conditions. Studies of pollen from peat or peaty soils (Godwin, 1941; Sears, 1938), human bones and artifacts, and vertebrate remains have received much attention in recent years.

Stream valleys in the periglacial zone commonly contain a series of terraces which can be correlated with times of glaciation by the tracing of terrace profiles into ice-margin deposits. Conditions for this type of correlation are especially favorable along streams draining alpine glaciers, as shown by the many studies in the European Alps. In a similar manner, lacustrine deposits along formerly ice-dammed streams can be correlated with ice advances. Commonly lacustrine deposits adjacent to waning glaciers contain varved clays. On the assumption that the varves present seasonal deposits, elaborate stratigraphic sequences based on an absolute annual chronology have been developed (Antevs, 1928; De Geer, 1940). Attempts made to correlate varve sequences of one continent with those of another have been made by De Geer and were summarized in monographic treatment in 1940. These long-distance correlations (telecorrelations) have been severely criticized by Antevs (1931; 1935) and others. In his comprehensive study and critical analysis of varves and "varvity", Hansen (1940, p. 418) concludes that many of the varves measured by De Geer

> "cannot be taken to be annual deposits or varves; they are sub-sections of annual deposits, registering shorter periods of change in the force of the water movement or in the quantity of the mud carried" and that, "sub-sections of this kind often occur in fairly conspicuous development in localities where the annual period itself has left no directly visible trace. This suggested interpretation means that *all distant or telecorrelations between Danish and Scanian varve localities mutually and between Scanodanian on the one hand and North American on the other, must be regarded as fallacious.*"

Recent studies of soil creep and related phenomena have been reported, but attempts to date these phenomena have been confined to correlations with the most recent periods of colder climate. Improved techniques and more information from detailed field studies may in the future indicate correlations with earlier advances.

Climatic fluctuations during the Pleistocene caused fluctuations of sea level in response to the amount of water withdrawn from the oceans and temporarily held in glaciers on the land. If the earth had been isostatically stable, these fluctuating sea levels should have produced world-wide shore features of erosion and deposition at relatively uniform elevations above or below the present datum. However, the earth is not generally stable and such ideal relations exist at only a few localities. Along with the normal crustal movements throughout the world there is also the added complexity of crustal warping and rebound in glaciated and peripheral regions, occasioned by the loading of the crust with ice (Daly, 1934; Lawson, 1940). Thus, the correlation of erosional and depositional features related to the various stands of the sea level are so complex that in regions remote from the glaciers relations to the various ages and subages of the Pleistocene are largely subjective, mainly based on numerical similarities in the sequence of events. In the periglacial and glaciated areas, correlation may rest on a much firmer basis, as shown by the excellent studies in the Baltic region (Sauramo, 1929; Tanner, 1930). Relationship between old shore lines and archaeological features have added fruitful stimulus to such studies and may prove especially helpful for correlation of features developed since the maximum advance of the last glacial age. Studies of ancient cultures along the New England coast indicate a slight elevation of the land, presumably due to isostatic rebound following the last glaciation (Johnson and others, 192; Johnson and Raup, 1947; R. P. Goldthwait, 1935).

Far from the sea shore, isostatic readjustment has resulted in tilting of the land following glaciation, as demonstrated in North America by measurement of the elevations of old shore lines on the Great Lakes (Leverett and Taylor, 1915; J. W. Goldthwait, 1924; Stanley, 1937; and others), Lake Bonneville (Gilbert, 1890; and others), Lake Champlain (Chapman,

1937), and glacial Lake Agassiz (deformation first recognized by Upham in 1884, but attributed to gravitative attraction of the ice sheet). Because of the position of these features within the limits of, or closely adjacent to, the last glaciation, the relation of old lake levels to the ice margins, ice-dammed or abandoned drainage channels, and other features, local sequences of events have been determined, but their position within an absolute chronology awaits further information. Similarly, the complexity of crustal movement along the west coast of North America prohibits correlation of Pleistocene gravel deposits now raised high above sea level with definite ages or subages of the Pleistocene. As pointed out by Flint (1948), the southeastern coast of the United States and the coast of Brazil are areas whose stability is such that, in the future, possible definitive correlations may be made between erosion and depositional features and the subdivisions of the Pleistocene epoch. Correlation of erosional and depositional features of streams related to various levels of the sea are believed to hold little promise for purposes of correlation because of the unique character of each stream in its adjustment to sea-level fluctuations.

Correlation of deposits in the periglacial zone is more satisfactory than in the zones farther from the ice, for here the correlation can be tied to ice advances and recessions which are of regional extent, or to fluctuations of sea level where crustal movements are such that they can be related to definite glacial times. Soils, loess, stream, and similar deposits have a regional extent which ideally lends itself to correlation with the sequence of events in glaciated areas at numerous points. Rarely have these deposits been given formational names, for they do not fulfill the qualifications used in the stratigraphic nomenclature for earlier geologic time.

Stratigraphy of Areas Remote from and only Indirectly Associated with Glaciation

In areas far from glaciated regions where there are no direct means of correlating events with ice advances and recessions, the problems of Pleistocene stratigraphy are manifold and difficult. Their solution must be based ultimately on climatic fluctuations which in these areas were generally not so large nor so important an environmental factor as in glaciated areas or the areas peripheral to glaciers. These climatic fluctuations apear to have produced either intensified or lessened precipitation along with temperature changes. Cool-moist periods are generally correlated with glacial ages, warm-dry with interglacial.

In areas of semiarid climate, generally located far from the sea, minor fluctuations in amount of rainfall produce notable changes in erosive and depositional processes, character of soils, and faunal and floral assemblages. Typical examples of such lake basins, as those in southwestern United States (Meinzer, 1922; and others), Africa (Nilsson, 1931; 1935; 1938; 1940) and elsewhere, are reported to show sequences of old shore lines indicating higher water levels during periods of increased precipitation (pluvial periods). Sedimentation in these lake basins may commonly show alternating beds of fresh- and salt-water deposits which, together with fossil assemblages, indicate changing conditions. Old spillways and drainage channels, stream terraces and associated stream deposits, and soil horizons can be correlated with the alternate raising and lowering of the lake levels. Periods of increased dryness may be correlated with periods of sand-dune and loess deposition, with attendant wind polish and scour on bedrock and production of ventifacts, or caliche and similar deposits. Increased rainfall may stabilize the dunes and produce weathering profiles in the soils and loess. Weathering will tend to destroy wind-polished and scoured surfaces and reverse caliche-producing processes. Changes in floral assemblages will be correlative with faunal changes. Changes in available food supply are especially well shown by migration of the larger animals and the predatory human being.

In areas of moderate to heavy rainfall, where fluctuations have less pronounced effects on the flora and fauna, dating and even definite assignment of events to the Pleistocene is difficult or highly speculative within the frame of our present knowledge. Stream terraces and deposits, gullying, and dissection are commonly assigned tentatively to the Pleistocene for want of definitive evidence. Soil horizons (Bryan and Albritton, 1943) and fossil and relict floras may indicate climatic conditions that differ

only slightly from those of the present. Without widespread horizon markers, such as layers of volcanic ash (Frye, Swineford, and Leonard, 1948), to which events can be related, correlation of events from watershed to watershed is difficult.

Occasionally fossil remains are uncovered in stratigraphic sequences that can be assigned to the Pleistocene, but whose exact position within the Pleistocene can be assigned only tentatively. Especially valuable paleontologic studies have been made of the deformed Pleistocene formations of California. (*See* Woodring and others, 1940; 1943; 1946). Often the character of the living fauna is not known, so comparison with fossil faunas assigned to the Pleistocene is not possible. Commonly migrations in altitude of the fauna is the only indication of climatic change (Stearns, 1942) unless extinction of the species is known. Where stratified deposits occur in caves or other sheltered and isolated positions, a sequence of events determined at one point may not be correlated with a regional sequence on other than a purely subjective basis. If sufficient events of major importance are noted within a single deposit, a common but hazardous practice frequently used to determine the age of the deposit is the correlation of the number of events in the local deposit with the number of events in the far-removed glaciated regions.

To evaluate qualitatively the importance of adaptations to environmental changes produced through climatic fluctuations, it is essential to know (1) the magnitude of these fluctuations necessary to change the environment significantly, and (2) the relative sensitivity of fauna, flora, soil, erosive processes, and other factors to these changes. Until more is known of the relative sensitivity of the various indicators of climatic fluctuations, interpretations of the past can be only subjective.

Submarine Stratigraphy

Within the past few decades increasing attention has been devoted to the study of the stratigraphy of the sea floor. High hopes are entertained that through this relatively new line of attack many of the problems of Pleistocene stratigraphy may be solved. Special techniques have been devised for obtaining submarine core samples of the unconsolidated sediments on the continental shelf that record the sequence of events dating back from the present (Bradley and others, 1942).

On the assumption that Pleistocene climatic fluctuations produced world-wide fluctuations of the temperature of sea water, it is logical to believe that there were resultant changes in faunal assemblages and sedimentation at any given locality. Migration of certain forms or marked changes in the composition of the fauna, primarily Foraminifera, indicate such changes in environmental conditions, presumably the water temperatures (Bradley and others, 1942; Phleger, 1939; 1942; 1945; 1947; 1948; Phleger and Hamilton, 1946). Lowering of sea level by the withdrawal of vast quantities of water stored in ice on the surface of the land produced changes in sedimentation (Trask, Phleger, and Stetson, 1947). Although there is no quantitative information available, salinity of the sea water must have been somewhat increased. Sedimentation on the continental shelves was materially affected by the changed strand lines. Likewise, the changed regimen of streams affected sedimentation, especially near stream mouths (Fisk, 1944). Similar changes, as yet little known, must have occurred where glaciers debouched directly into the sea.

Results of recent studies of the sea-floor deposits have been summarized by Phleger. He reported (1948) that one core, 15.4 meters long, taken from the Caribbean, showed 11 obvious shifts to a cold-water environment, perhaps giving a complete stratigraphic section of the Pleistocene climatic fluctuations. A speculative, but highly fascinating attempt is made to correlate stratigraphic sequences indicating warm- and cold-water phases with the climatic fluctuations which produced the glacial and interglacial ages and subages. No attempt has yet been made to name submarine formations or to establish definite correlations on the basis of changing faunas. It is hoped that, with further study, the records gathered from many points on the sea floor may be correlated on a world-wide basis, thus giving the first definite information regarding a world-wide chronology which must be correlative with that developed by the study of terrestrial deposits.

Summary

Many branches of science have a vital interest in the Pleistocene epoch, which is defined and characterized by multiple climatic fluctuations. These fluctuations have left myriad impressions which range from the spectacular features of glaciation to the almost imperceptible changes in regions far removed from glacial conditions. All life, the environment, and the attendant physical processes were influenced by the sequence of climatic fluctuations on which Pleistocene stratigraphy ultimately must be based.

Techniques differ from those used in the stratigraphic interpretations of earlier geologic time. Local sequences of events can be established, but not always can they be fitted definitively into the major chronology. The establishment of a world-wide chronology with uniform terminology has not been attempted and would be hazardous with the present state of knowledge. Because of the localization and character of Pleistocene deposits, formational names are less commonly applied than in earlier geologic time. In general, correlation of deposits has been attempted by reference to the various periods of cold or warm climate, referable to glacial or interglacial age or subage.

Each field of natural science dealing with the Pleistocene is striving to establish a chronology into which the sequence of events of the individual sciences can be fitted. However, independently, none can give the complete answer. Each field of specialization, as in the case of stratigraphy, needs the direct aid and support of all others in order to derive a chronology applicable to all. Ultimately this chronology will rest on the series of world-wide climatic fluctuations, of which, unfortunately, neither the cause nor the detailed story is now known.

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PLEISTOCENE RESEARCH

A REVIEW BY THE MEMBERS OF THE COMMITTEE ON INTERRELATIONS OF PLEISTOCENE RESEARCH, NATIONAL RESEARCH COUNCIL

10. ALPINE GLACIATION

BY LOUIS L. RAY

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INTRODUCTION

Until the close of the eighteenth century, the forbidding summit areas of the great Alpine mountain chain of Europe held unknown terrors for men in all walks of life. Few strayed from the ancient routes of travel through the passes; glaciers and perennial snow, nestled among the rugged peaks, were shunned. Not until the early nineteenth century did naturalists, spurred by the pioneer studies of De Saussure, discover the beauty and scientific interest of the ice and snow fields. The avid exploration and inquiry of naturalists and philosophers in the Alps marked the opening of an early period of investigation which culminated in the charming essays of Tyndall.

These early students of Alpine glaciers recognized that rock debris transported by glaciers and discharged from the melting termini indicated that glaciers are active agents of erosion, modifying the terrain in conformity with definite dynamic processes. The slow motion of the ice, creeping down the valleys, led to the conclusion that ice acted much as a stream of water, smoothing and polishing the bedrock over which it moved and modifying the landscape by shaping the terrain. Glacier-transported debris, deposited directly from melting ice or by meltwater streams, left unmistakable evidence of past fluctuations of the glaciers within the valleys and far from the glacierized areas along the courses of the drainage streams.

Albrecht Penck and Brückner, in Europe, and W. M. Davis in America, through their classic studies in the opening years of the twentieth century, formalized the study of features of alpine glaciers.[1] The tremendous imprint of their studies so fixed the general ideas concerning alpine glaciation that for many years little attempt was made to re-examine or challenge their beliefs. Recently, detailed studies of some processes indicate the necessity of minor revisions. The main concepts, however, remain essentially unchanged.

Through the erosional and depositional features of the landscape, produced by episodes of alpine glaciation, the geologist can reconstruct the glacial history. Because these episodes of glaciation are the result of climatic fluctuations, on which the geologic history of the Pleistocene, as well as the epoch itself, is based, interpretation of the geomorphic development of the landscape by means of alpine glaciation leads to the development of a chronology of climatic events whose impact on many other fields of science concerned with the Pleistocene is essential to their interpretation. To the development of this chronology the information supplied by studies of alpine glaciation is especially important. Many problems of

[1] "A glacier formed among summits and descending a mountain valley." Webster's New International Dictionary of the English Language, 2d ed., unabridged: G. and C. Merriam Co., Springfield, Mass., 1946.

alpine glaciation, either poorly understood or in need of more detailed study, are emphasized.

The Cirque

Until the classic study of W. D. Johnson (1899), opinions differed widely as to the processes that produced the cirque. It had been suggested that they were of preglacial origin, that they were weathering features, that they were produced by water erosion, that they were shaped by the action of ice, and that avalanching of snow and ice to the cirque floor produced erosion similar to that beneath a waterfall. Johnson's observations led to the general acceptance of his *bergschrund hypothesis*, that cirques are the product of basal sapping of the walls of a depression in which snow accumulates. Descending a bergschrund (the crevasse which commonly parallels the headwall of the cirque during the warmer months at the point separating stationary from moving snow and ice), he found that the crevasse penetrated to bedrock and that its lower part separated bedrock on one side from moving ice on the other. His observations showed that meltwater resulting from the warm, day temperatures kept the rock of the headwall wet. Air circulating through the bergschrund during the summer months is subject to diurnal changes, frequently crossing the freezing-thawing point. At night, when temperatures drop below freezing, melt water is changed to ice, causing appreciable mechanical disintegration of the bedrock cirque headwall. Blocks riven and pried from the headwall by ice action are incorporated into the moving ice on the down-valley side of the bergschrund and are transported from the cirque. This process of sapping of the cirque walls long has been accepted as the casual factor for the development of the cirque after initiation of the depression for snow and ice accumulation, either through preglacial weathering and erosion or through the process of nivation, described and named by Matthes (1900).

W. V. Lewis (1938; 1940) questioned the ability of bergschrund sapping to produce precipitous cirque headwalls from several hundred to 2000–3000 feet high. Because the thickness of ice within the larger cirques exceeds the critical thickness for producing plasticity in the lower layers (Perutz, 1948), Lewis reasoned that the bergschrund could not remain open at a depth sufficient to produce the observable headwall sapping. His observations of many cirques now occupied by glaciers, the restoration of the surface gradient of ice within deglaciated cirques, and the relation of the snow surface to cirque walls have led Lewis to modify the bergschrund hypothesis and to develop a more comprehensive *meltwater hypothesis*. In brief, this hypothesis explains

> "that meltwater periodically descends the headwalls of cirques, melts its way down behind the ice and into crevices in the rock, and there freezes at night or during cold spells. The material thus broken loose is then removed by the glacier, and cirque erosion proceeds mainly by this form of headwall recession" (Lewis, 1949, p. 110).

D. W. Johnson (1941) severely criticized the meltwater hypothesis, clinging to a slightly modified bergschrund hypothesis, confining headwall erosion to the bergschrund. Lewis' convincing reply (1949) has opened a broad front on which to attack, from field observations, the validity of the arguments, not only from the viewpoint of existing glaciers in differing climatic zones, but from that of the Pleistocene, when the climate was more rigorous.

Ahlmann (1935; *see also* Matthes, 1942) has classified glaciers as *high polar*, *subpolar*, and *temperate*, depending on their geographic position and thus their relation to temperature conditions. Little is known concerning the effects of these temperature conditions on geomorphic processes of existing alpine glaciers. If effects show marked differences in processes active in the different types, then similar differences may be discovered in geomorphic features in alpine glaciation which may be referred to the fluctuating climatic conditions of the past. Possibly such processes of cirque formation as outlined by the meltwater hypothesis may not function for all three glacier types. Observations should be made where possible that may have bearing on this critical problem.

The rate of downward cutting of the cirque floor, as contrasted with the headward recession of the cirque, has received considerable attention, especially because of its close relation to the method of cirque formation (Cotton, 1940). D. W. Johnson's assumption (1941) that a cirque glacier lowers the floor of the cirque

more rapidly than it saps its headwall has been answered through numerous field observations in Norway by Lewis (1949, p. 125) who points out that,

"In both the Rondane and Jotenheim one constantly finds that the cirque floors grade, without any significant break of slope, into the plateau surface—*flye*—that surrounds the higher monadnock masses. As many of the cirque glaciers probably originated in the angle between the plateau surface and the upstanding masses, it does not seem that much downward erosion has accompanied their substantial recession into these masses."

Commonly small lakes occupy depressions in cirque floors. Often, ice-free cirques may have lakes lapping directly against the headwall; in others, still containing small ice masses, lakes may lie between the ice margin and the bedrock lip. Although such basins and bedrock lips have been frequently described and attributed to pecularities of glacial erosion, little attempt has been made to understand their origin. Studies by Lewis (1948; 1949), however, have given a rational mode of origin through rotational slipping of the ice mass along thrust planes in cirque glaciers too thin for plastic flow. Movement is analogous to landslide caused by overloading or oversteepening of bedrock. A series of thrust planes, probably following seasonal zoning bands in the ice, have been reported by many to emerge from small cirque glaciers at relatively steep angles, dipping toward the valley head (Gibson and Dyson, 1939). Lewis suggests that the weight of snow accumulating each season between the margin of the névé and the headwall, and the melting at the snout of small glaciers, may upset the equilibrium so that a rotational movement occurs along an arcuate thrust plane more or less parallel to the bedrock-ice contact. Debris derived from the headwall and frozen into the ice provides ready tools for abrasion of the cirque floor. He suggests (1949, p. 128) that,

"The tendency to form arcuate glide planes is probably the main reason for the development of the basin form with its reversed slope, because toward the sill the ice tends to remove upward and so to reduce the scouring of the floor at that point."

In glaciers moving far out of the cirque, the rotational slipping might still occur with favorable conditions, thus giving rise to a series of valley steps and basins. As, however, such rotational slipping requires a steep surface gradient of the ice, the most favorable area is near the cirque. This is substantiated by field evidence. Where bedrock character is most suitable, development of valley steps is accelerated, as discussed later.

The Glaciated Valley

Probably the most spectacular feature of glaciated mountains is the glaciated valley leading from the cirque. Its relatively low gradient (except in the stretch immediately below the cirque), its U-shaped profile, hanging tributary valleys, polished bedrock surfaces, bastions, basins, rock steps, riegels, roches moutonnées, and other features are characteristic of alpine glaciation. Each feature is the product of glacial erosion or a modification of a pre-existing landform; similarly, glacial deposition produces characteristic features within the valley. Each has been studied and discussed; some features are not adequately explained.

The long profile of a glaciated valley differs from that of the nonglaciated valley in that the gradient is generally less in the lower part and steeper in the upper, especially near the cirque, where the steep gradient may be accentuated by precipitous bedrock steps. Since glaciers have merely modified pre-existing valleys cut by mountain streams, differences in gradient are primarily the result of glaciation.

Glacial deepening of a valley is accomplished by (1) abrasion, and (2) plucking or quarrying. The predominance of one form depends largely on the character of the bedrock. Where bedrock is massive, abrasion is dominant. Where bedrock is well jointed, plucking is dominant. By the wedging action of meltwater freezing in joints in bedrock beneath the ice, blocks are pried out and incorporated into the overlying, moving ice. Doubtless the plucking action of glacier ice is far more effective for valley deepening than abrasion, which may appear to be more important because of the obvious smoothed and polished surfaces left after deglaciation.

In the zone of ice accumulation and that part of the valley immediately below, bedrock erosion by ice is greatest because movement is most rapid through the action of gravity, aided by plastic flow in the lower ice of the larger glaciers. It is suggested that the glacier

tools, in the form of angular bedrock fragments derived by sapping and plucking of the cirque walls and floor, may perhaps be more efficient as agents of abrasion of the valley floor than when more rounded, following continued abrasion in the lower parts of the glacier, as sandpaper of angular fragments is more effective than that of rounded fragments. No study of this possible variation in effectiveness of the glaicer tools is known.

In the upper part of a glaciated valley glacial erosion is more effective than in the lower part, where ablation thins and destroys the glacier. Reduction of the amount of ice and rate of movement because of the decreased impetus of gravity tends to flatten the valley profile. Local variations from the typical gradient may result from many causes such as bedrock steps, constriction of the valley walls, and entrance of tributary glaciers to the main valley. At these places glacier movement would be more rapid with consequent increase in glacial erosion. Exceptions to the normal valley profile are numerous, but do not negate the general principles of glacial erosion. Classic examples of such changes in profile have been described by Matthes (1930) in the Yosemite Valley.

Not only does glaciation deepen the preexisting valley, but, as the glacier may fill the valley bottom and extend high up on the valley walls, glacial erosion vigorously attacks that part of a valley not subject to normal stream erosion. In consequence, the glaciated part of the valley tends to be shaped to that form which permits the greatest volume of ice to flow with the least frictional resistance—that is, to a semicircular profile. Furthermore, glaciers tend to straighten valleys by removing spurs and other irregularities which would impede ice movement, thereby producing more or less straight troughs with truncated spurs along the lower, oversteepened valley walls (Cotton, 1941; 1942). Only where valley floors are free of debris can the semicircular shape be distinguished; most glaciated valleys are choked with deposits which tend to produce a flat floor and accentuate the steepness of the valley walls. The general form of the glaciated valley and its development was described long ago by W. M. Davis and others, and has received little qualitative study in the past few decades. Cotton (1942) has presented an admirable review of many aspects of glaciation.

The U-shaped valley may be highly irregular because of differences in bedrock resistance to erosion and differences in effectiveness of glacial erosion. The effectiveness of erosion may be modified by such factors as position relative to the ice mass as a whole, amount of load used by the ice as abrasive tools, configuration of valley and thus differences in rate of movement, and confluence of tributary glaciers with the main trunk glacier. For example, a large glacially rounded bedrock mass, projecting from the valley wall immediately downvalley from the junction with a tributary glacier, has been termed a *bastion* by Von Engeln (1937) who believes (*see* Cotton, 1942, and Ives, 1946) that bedrock of the valley wall has been protected from the severe glacial erosion of the trunk glacier by the thrust of the tributary glacier at right angles to that of the trunk glacier. Field evidence indicates that, although the tributary glacier joined the trunk glacier discordantly, the surface levels of the two may have been near accordance.

Many minor roches moutonnées-like irregularities, to which names such as *knob fields*, *semi-detached knobs*, *sugarloaves*, or *beehive forms* are applied, are nestled on valley floors or walls. References to many of these minor features of glaciation are scattered throughout the voluminous literature. Cotton (1941; 1942) reviews these features, together with many references to earlier studies. Drainage along lateral and terminal margins of the alpine glaciers may often have been complex, especially during deglaciation. Box canyons may cut across bedrock spurs and bedrock masses emerging from beneath the melting ice (Ray, 1935). Such features are common to all regions of mountain glaciation, but are frequently only casually mentioned in the literature.

When a main stream valley is glaciated, it is deepened sufficiently so the junction of a tributary with the main valley is not accordant, and the tributary valley terminates or hangs above the main valley floor on the valley wall. It is not necessary that the tributary valley be glaciated, for the larger glacier occupying the main valley will have deepened its valley faster than the tributary. Matthes (1930

showed, by profiles projecting the gradients of the hanging valleys to the axis of the main valley, that hanging valleys are largely due to deepening rather than to widening of the main valley by glacial erosion and oversteepening of the valley walls. The latter process may, however, account for some of the slightly discordant valley junctions.

Cotton (1945) has pointed out that, when both main and tributary valleys were ice-filled and glaciers were largest, the junction of the ice masses was accordant and tributary glaciers did not generally join as ice falls. He says (1945, p. 318–319),

> "In an accordant junction, . . . whether it be of ice streams or water streams, it is the surfaces of the streams that join at grade. There is a tendency both in glaciers and in rivers to adjust the size of every cross-section of the channel to suit the volume of ice or water that must pass through it. . . . The glacier tributary has a smaller cross-section, and is thus shallower, than the main, and so the floor of the tributary valley must be at a higher level than that of the main, so that it forms a hanging valley when no longer occupied by the ice."

In general glacier surfaces may have been accordant at the time of maximum expansion of valley glaciers. However, more rapid deepening of the main valleys than of the tributaries would tend to produce ice falls, and later water falls at the valley junctions.

Since Matthes' classic work on Yosemite Valley (1930) there has been little critical geomorphic study of the hanging valley. A critical review of this problem, especially in such areas as the Alps, appears warranted.

Glaciated valleys are commonly characterized by a series of bedrock steps and basins, especially in the headwater reaches, so the long profile may appear like a stairway, the risers of bedrock, from a few to several hundred feet in height, separating flattish treads commonly occupied by bedrock basins. Various widely divergent theories have been advanced for the origin of these features, some of which have been summarized by Lewis (1948) in his critical analysis of the problem.

A few of these theories are outlined to indicated differences in basic principles proposed. W. D. Johnson (1904) suggested that the steps were formed by meltwater descending to bedrock through deep transverse crevasses in the valley glaciers. The freezing and thawing of the meltwater, entering openings in the bedrock at the bottom of the crevasses, wedges out blocks which can then be incorporated into the overlying moving ice. Thus, a bedrock step, developed at the site of the crevasse, moves slowly upvalley with continued glaciation. Garwood (1910) believed that bedrock steps were due to glacial protection rather than erosion, each step marking the position where downcutting by streams emerging from beneath the glacier had been halted in interglacial time by the protecting glaciers. In 1922, Taylor proposed the *palimpsest theory* on the basis of his observations in Antarctica, believing that the steps originated as the headwalls of a series of independent cirques, later integrated into a single stepped valley. Sölch (1935) proposed that the steps mark the heads of streams rejuvenated by periodic uplift.

Matthes (1930), after detailed study of the glacial features of Yosemite Valley, concluded that, as the steps coincided with zones of less-jointed bedrock, they were due to bedrock resistance to glacial erosion; excavation of the well-jointed bedrock produced the treads. This explanation is in harmony with the principle of selective quarrying by glaciers. Unfortunately, bedrock jointing in other glaciated valleys where steps occur has not been studied, and Matthes' explanation has been accepted generally without further proof.

Lewis (1948), in offering several hypotheses for the formation of valley steps, enlarged on the explanation of Matthes by applying his principle of meltwater sapping to the quarrying of bedrock where glaciers are sufficiently thin to expose parts of the bedrock of the steps and permit the entrance of meltwater beneath the ice, thus evoking the same sapping and quarrying effects by which he explains the origin of cirques (Lewis, 1938; 1940). Where glaciers are thick, Lewis held that a small amount of glacial sapping and quarrying may be aided by the hydrostatic pressure of meltwater in openings in bedrock and the freezing of meltwater as pressure is released on the stoss side of bedrock irregularities by movement of glacier ice. Lewis also inferred that extrusion flow may account for bedrock irregularities, for, where the ice is thickest, its movement is dominantly by extrusion flow

and thus greatest in the lower parts of the glacier. Assuming that, where velocity is greatest, scouring and grinding are at a maximum, basins would be formed at the base of steps, on the treads. Lewis' mechanism of rotational slipping is also suggested as a factor in the production of valley steps, following the same lines of reasoning and observation used in his suggestions concerning the formation of cirques.

Commonly a bedrock barrier or *riegel* may extend across a constricted section of a glaciated valley at the brink of a bedrock step. These have been described mainly from the Alps where they frequently coincide with resistant bedrock strata, thus suggesting that they may be remnants of preglacial landforms. Older workers, such as W. M. Davis and Albrecht Penck, explain riegels by glacial overdeepening. De Martonne, suggesting that riegels occur where valleys are constricted, relied on bedrock resistance to glacial erosion and preglacial stream rejuvenation (Cotton, 1941;1942). No generally acceptable theory has been devised to explain their origin, and it may be that riegels have been produced by several means. However, valley-step formation and the relation of ice movement to efficiency in erosion of bedrock of varying resistance (Lewis, 1938; 1940; Matthes, 1930) may indicate more clearly the production of the riegel.

Valley steps and riegels may be formed by several processes; in each case the condition of bedrock and the glacier must be analyzed. Confirmation of the mechanisms recently proposed must await more thorough knowledge of the physics of ice movement, effectiveness of meltwater beneath the glaciers, and details of the bedrock formations.

Basins, common in glaciated valleys, are generally assigned to several of the formative processes that produce the valley steps, such as selective quarrying of shattered bedrock, extrusion flow, and rotational slipping. However, many have been explained by greater ice velocity due to constriction of the valley and the entrance of large tributary glaciers to the trunk glacier, both producing a greater velocity of the ice and thus more effective erosion. Thus, like the valley steps, basins may be assigned to several processes, depending on the local conditions of bedrock and ice movement.

The relative effectiveness of glacial abrasion and quarrying in producing these various features and in the sum total of glacial erosion is variable, depending on local conditions of bedrock character and ice. Generally, quarrying has been the greatest erosive process, being the greatest amount of rock, although in places abrasion has been interpreted as most active (Daly, 1912). Smoothing and polishing of bedrock are so obvious that often the amount of bedrock removal has been assessed on surficial features alone. Matthes (1930) and Jahns (1943) have indicated the relationship between bedrock character and amount of quarrying. Unfortunately, detailed quantitative studies are relatively few; in the spectacular fjord regions, where erosion has been intense and careful results are necessary for understanding mode of origin, conclusions are diverse. It is hoped that detailed geomorphic studies, correlated with studies of bedrock character and restoration of former ice conditions, will aid in bringing about the necessary specific information on the effectiveness of abrasion and quarrying, as well as the total capacity of a glacier to erode, both vertically and laterally.

Deposits of Alpine Glaciers

All debris transported by an alpine glacier is deposited in a variety of forms and in one of two ways—either directly from the melting ice or through transportation by meltwater drainage streams (fluvio-glacial). Interpretation of the origin and significance of the deposits is necessary to understand the sequence of local events and the position of these events in the world-wide glacial chronology.

Lateral moraines may form conspicuous ridge-like features of unsorted debris. Rock fragments transported by the glacier and concentrated along the valley walls by melting of the ice are augmented by debris fallen from the valley walls, where weathering is unusually active because of the climatic conditions favorable to it. Cotton (1942) has termed those ridges that lodge on benches or other locally level areas along the valley walls, *stranded moraines*.

Unfortunately, there has been little critical investigation of the origin and significance of lateral moraines; some of the complexities have been discussed by Flint (1948b) in his study of South Glacier on Jan Mayen. Although

lateral moraines have been used to establish glacial ages, especially where terminal moraines have been removed by erosion (Ray, 1940), care must be used in separating a series of such moraines. As Flint has noted on Jan Mayen, each morainic ridge does not necessarily represent an ice advance. If lateral moraines merge with terminal moraines, more exact dating and the establishment of a sequence of ice movements may be possible.

Medial moraines, commonly described from observations of existing glaciers, are rarely preserved during deglaciation. Because their final lodging place is the valley floor, the debris is subject to intense stream erosion and removal, or burial beneath fluvio-glacial deposits. Formed by the merging of lateral moraines at the confluence of two glaciers, medial moraines may attain spectacular development on existing glaciers, although near the distal margin the debris may be so scattered as to lose its identity and merge into a superficial ablation mantle, of little value in the determination of the glacial history.

Few students have distinguished critically between the *terminal* or *end moraine*, marking the farthest advance of the glacier at a given age, and the *recessional* or *stadial moraine*, marking a position in the recession of the glacier when the ice stood almost stationary for a time sufficient to permit building of a moraine. The size of these moraines depends on a variety of factors and not alone on the size of the glacier or the amount of load that it transports (Cotton, 1942). In New Zealand, the absence of moraines in many valleys may be accounted for, according to Speight (1940, p. 140), in several ways:

> "(1) Such a moraine has never been deposited . . . ; (2) A terminal moraine was deposited but destroyed subsequently by the action of the glacial stream; (3) The terminal moraine, if formed, was buried in the material brought down by rivers; (4) Deposition of the burden of debris has taken place by downwasting, the covering material having just been dropped as the ice wasted away."

Little attention has been paid to the minor features associated with the terminal moraines: solifluction layers, ventifacts and other eolian features, depth of weathering, and erosion. These should be examined in detail, especially where moraines are used for determination of a glacial chronology. Evidence on which determinations are made concerning origin and age relations of a moraine, whether it marks a halt at a maximum position of advance, or a halt in the recession from a more advanced position, is still subjective. Supporting evidence is usually gathered elsewhere, especially from related fluvio-glacial deposits (Bryan and Ray, 1940).

Almost all alpine glaciers have been receding since they were first studied in detail (Ahlmann, 1948; Matthes, 1942). Thus, there is little definite information on the differences in amounts of meltwater and debris issuing from an advancing, as opposed to a receding glacier. However, once the terminus of the ice extends below the snow line, large quantities of meltwater are produced, and debris is freed and washed from the melting ice. The larger the ice tongue and the greater its length below the snow line, the greater the amount of meltwater and debris.

The ice-freed debris is transported, sorted, and commonly re-sorted many times by meltwater streams. Deposits of many types are developed, both adjacent to and far from the terminus of the ice, along the courses of the meltwater streams. Because of the areal extent, fossil content, relation to other datable deposits, weathering, and erosion, the fluvio-glacial deposits form an important key to the interpretation of the history of alpine glaciation.

When alpine glaciers have pushed from their confining valleys on to piedmont lowlands, outwash spreading from the ice margin forms broad aggraded *outwash plains*, *fans*, or *aprons*. These features have been likened to alluvial fans developed by continuous rather than intermittent upbuilding (Von Engeln, 1942). If the glacier terminus remains fixed for a long time, aggrading streams may build up the debris to the level of the ice surface; perhaps debris may be deposited on the ice itself (Mannerfelt, 1945). Detached blocks of ice may be incorporated within the fluvio-glacial deposits so that when melting occurs the sediments will be let down in irregular masses to produce pitted outwash plains with kettle holes and related features (Wentworth and Ray, 1936).

If the glacier terminus stagnates or retreats slowly from its advanced position outside the confining valley walls, gradients of the drainage streams may be lowered and debris load diminished so local terrace sequences may be

developed in the outwash plain near the ice margin (Ray, 1935). If recession is rapid, a fosse may be developed between the melting ice and the terminal moraine or inner ice-contact margin of the outwash plain. This fosse, filling with meltwater, produces a proglacial lake in which sediments are so deposited that there are commonly intimate mixtures of unsorted debris from the moraines, sorted stream deposits, and lacustrine deposits. Meltwater drainage streams, dropping their heavy load in the lake basin, issue as underloaded streams capable of further trenching of the outwash debris. By these methods a series of small terraces may be developed near the glacier terminus; downstream, far from the glacier, they may merge into a single terrace representing the major ice advance.

Debris carried far from the glaciated areas may lose its glacial character through the gradual reshaping by rounding, comminution, and adulteration by nonglacial sediments of tributary streams draining nonglaciated regions. Climatic fluctuations and consequent fluctuations in the glacier regimen may produce terrace sequences along streams far from the mountain areas. These sequences in nonglaciated areas may be traced upstream and correlated with glacier advances marked by morainic systems in the mountain valleys or piedmont lowlands (Bryan and Ray, 1940).

Where glacier termini are confined within valley walls, the debris carried from the ice commonly floods the valley from wall to wall, producing a *valley train*, correlative with extensive terrace levels far from the glaciated areas and with the terminal or stadial moraines within the valley. Correlation of major and minor terrace sequences should be studied in detail in areas of existing glaciers so that interpretation of similar sequences developed by former ice advances may be properly interpreted, for they are generally the most important means of recovering the sequence of events in the history of an alpine glacier.

The walls of valleys formerly occupied by alpine glaciers are commonly oversteepened and subject to severe weathering, so unconsolidated debris, deposited on them at the time of glaciation, is rarely preserved. However, studies of existing glaciers demonstrate that, during deglaciation, a wide variety of features are formed by deposition between the lateral ice margin and the valley wall. Sediments derived from the debris of the lateral moraines, from the valley walls, and from the surface of the glacier are sorted and deposited along lateral stream courses. These deposits are similar to, but smaller than, the kame terraces formed during deglaciation of the continental ice sheets along stream valleys. Where drainage is blocked, small lakes may be formed in which lacustrine deposits accumulate (Mannerfelt, 1945). With reduction of the glacier ice or drainage of the impounded water through subglacial channels, the lateral deposits may be stranded on the valley walls. Their unstable position and unconsolidated character commonly result in their rapid disappearance through slumping and erosion.

As deglaciation progresses, valley walls may become blanketed with remnants of lateral deposits from the highest point of deposition to the valley floor. Lateral drainage channels cut in both bedrock and surficial debris have been described by Mannerfelt (1945) from the valleys of Scandinavia. Where they occur in sequences on the valley walls—as many as 78 have been reported—he suggests that they are annual features, the result of seasonal ice melting of an almost catastrophic nature. Until the exact nature of deglaciation is thoroughly known, many of the problems will remain unsolved. Studies similar to those of Mannerfelt should be made in other regions in the hope that fundamental principles may be established.

Deltas in the proglacial lakes and lacustrine deposits in the basins of mountain valleys should receive more detailed study from the glacial geologist and the sedimentologist because of their close relation to the chronological history of the region and the fluctuating physical environment. This is especially true in regions where paleontological and archaeological finds may be closely associated with the sedimentary history, both chronologically and geographically.

The Glaciated Mountain Landscape

Davis' classic paper (1906) on the sculpture of mountains by glaciers is a lucid explanation of the character of glaciated, as opposed to nonglaciated, mountains. Since this early ex-

position and Davis' many later papers, there have been numerous reaffirmations, minor modifications, and additions to the original thesis (Ahlmann, 1919; Cotton, 1945; Hobbs, 1911; and others), now universally accepted. Later literature on the over-all sculpture of the mountain landscape has been largely descriptive and confirmatory. Even the diagrams of Davis (1906, p. 80, 81, 83) illustrating the development of the glaciated mountain landscape through three stages, from (1) nonglaciated, to (2) glaciated, and to (3) deglaciated, have frequently recurred in the literature in their original or modified form (Cotton, 1945; Hobbs, 1911; Flint, 1948a).

The erosional capacity of glaciers, like that of running water, may be considered cyclic in its role as modifier of the landscape. Theoretically, if mountains are elevated to heights producing glaciation, the glaciers should in time remove the summit areas of accumulation by erosion, reducing the mountains to elevations at which the glaciers could no longer sustain themselves, and would thus disappear. As Davis has pointed out (1906), this cycle of erosion, from birth to extinction of glaciers through their reduction of the land surface, is not known to have happened, and, in mountains such as the Alps, the strongly glaciated terrain with rugged peaks and aretes characterizes a landscape which was more intensely glaciated in the past. Thus, episodes of glaciation have never lasted long enough to reduce mountains sufficiently to cause extinction of the glaciers, and glaciation is therefore the product of an external control—climatic fluctuations.

Davis, in his many publications, Hobbs (1911), and others have described the production of the many rugged forms such as horns and aretes, that are characteristic of the glaciated mountains. These forms are either directly or indirectly the result of glaciation and the transformation and removal of the gently rounded uplands by consumption through headward expansion of the cirques. Davis held that glacial features will be rapidly replaced by "normal" features following deglaciation. However, if a second glacial episode follows the first, "the amount of sculpture effected in a first glacial epoch may therefore be reasonably estimated as of much greater volume than in a second epoch" (Davis, 1906, p. 82). Thus, fluvio-glacial and most minor features of a glaciated valley or mountain terrain are either produced by the last epoch of glaciation or have been highly modified by the last glaciation from pre-existing glacial forms. Many regions where alpine glaciers existed may have been later overwhelmed by extensive ice caps or even continental ice; the features of alpine glaciation now observed may be the earlier forms resharpened by glaciation in a later period of climatic refrigeration. Too little is known of the processes of deglaciation and reglaciation, as witnessed by the controversies concerning the origin and age relations of the cirques in the White Mountains of New Hampshire to the continental ice sheets (Goldthwait, 1940; D. W. Johnson, 1933). This type of problem has, however, recently been studied in Norway and Sweden (Mannerfelt, 1945). Careful consideration should be given to such studies so that this vexing problem may be clarified and the effectiveness of glacial mountain sculpture may be more thoroughly understood.

Summary

Alpine glaciers are important molders of the terrain, producing a variety of erosional and depositional landforms. Through these, the history of climatic fluctuations, to which the glaciers owe their existence, may be deduced. Because alpine glaciers are of limited extent and mountains supporting them are widely separated geographically, the alpine glaciers carry the evidence of climatic fluctuations far from the areas of continental glaciation. Moreover, climatic fluctuations too small to produce vast continental glaciers may be sufficient to produce minor advances of alpine glaciers and landforms, as historic evidence indicates. For this reason, deposits of alpine glaciers, far from the border of the continental drift deposits, may carry the glacial chronology of major and minor climatic fluctuations into areas for which no other datable sequence of deposits exists. Not only are alpine glaciers an important geologic factor in the dynamic processes affecting the higher mountains of the earth, but they are an important key to the understanding of the Pleistocene.

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PLEISTOCENE RESEARCH

A Review by the Members of the Committee on Interrelations of Pleistocene Research, National Research Council

11. PHYSICAL EFFECTS OF PLEISTOCENE CLIMATIC CHANGES IN NONGLACIATED AREAS: EOLIAN PHENOMENA, FROST ACTION, AND STREAM TERRACING

By H. T. U. Smith

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Introduction

Climatic change constitutes the common denominator for a wide range of Pleistocene[1] phenomena. Recurrent glaciation was by far the most spectacular of these phenomena, and its records, gradually deciphered over a long span of time, provide the basis for a standard chronology of the Pleistocene. Beyond the glacial border, the effects of climatic change, although far-reaching, were for the most part less dramatic and are therefore more difficult to distinguish. Investigation of these effects,

[1] In this paper, the term Pleistocene is used to include all of post-Pliocene time, as proposed by Flint (1947, p. 209).

however, is essential for an understanding of the Pleistocene in its broader aspects. To a considerable extent, it is on the basis of relations to a sequence of climatic changes that events in the nonglaciated areas may be correlated with one another and with the standard time scale, allowing the many local and limited chronologies to be drawn together in a unified picture of Pleistocene history. Furthermore, it is mainly from a study of climatic effects in the nonglaciated areas that we may expect to gain a more adequate conception of the character and magnitude of the climatic changes themselves, thus to obtain a better basis for reconstructing meteorologic conditions attending glaciation, and for considering their bearing on theories as to the ultimate cause of Pleistocene climatic fluctuations.

Climatic effects in nonglaciated areas are recorded in two main types of phenomena: biologic and physical. Investigations of the biologic phenomena, involving the migration and progressive modification of floras and faunas, are fundamental and are dealt with elsewhere in this series of papers. The evidence provided by purely physical phenomena complements the biologic record and, in the many places where fossils are absent or inadequate, provides the primary basis for interpretation of former climatic changes. Of the various physical effects related to climatic fluctuations, three are of particular interest for the problems which they present and for their significance in the interpretation of the Pleistocene record: (1) eolian phenomena, including dune building, loess deposition, and sand blasting; (2) frost phenomena, including mechanical weathering, ground-ice development, solifluction, and associated processes; and (3) stream terracing produced by alternations between aggradation and degradation. In this paper, each of these types of phenomena is discussed from the viewpoint of its relevancy to the interpretation of Pleistocene events. The discussion is designed (1) to review the present status of investigations in each field and to provide a guide to the literature relating to it; (2) to note some of the problems in need of study, with particular reference to the Pleistocene of North America; and (3) to suggest ways in which the co-ordinated efforts of workers in several related fields of science concerned with the Pleistocene may contribute to the solution of these problems.

In studying the physical effects of ice-age climatic conditions in nonglaciated areas, it has been found that certain effects are particularly prominent in a zone of indefinite breadth marginal to continental ice sheets. In this zone, the meteorologic regime is presumably influenced to a considerable extent by the ice itself, making for cold, frosty, and windy conditions. The zone thus characterized, as well as the general climatic conditions and geomorphic phenomena in that zone, is commonly designated as *periglacial*.

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Eolian Phenomena

Sand Dunes

Introduction.—In the study of Pleistocene geology, the dunes of direct interest are those which antedate the present—that is, those which either are stabilized at present or which, although now active, became so through rejuvenation following an interval of stabilization. From such dunes one can infer (1) former direction of dune-building winds; (2) former conditions of relatively greater aridity, or other conditions responsible for a source of sand; and (3) in certain favored localities, a sequence of alternations between dune building and stabilization or other processes. Dunes of strictly modern origin are of indirect interest insofar as they reveal characteristics significant for the interpretation of ancient dunes.

Attempts to make interpretations of this type began in Europe and date back to the early 1900's. In the earlier stages of investigation, considerable controversy arose on various points of interpretation. This was reviewed at length by Högbom (1923) and more briefly by Cooper (1935). Högbom's work did much to settle the controversy and to present a unified picture of late Pleistocene dune building.

In North America, dune studies are considerably less advanced than in Europe, although dune areas are far more extensive. Until recently, the few observations recorded were mostly casual and general. Undoubtedly this was due largely to the absence or inadequacy of maps for dune areas. With the advent of aerial photography a new method of attack was opened up, leading to definitive studies by Cooper (1935), Melton (1940), H. T. U. Smith (1940a; 1940b), and Hack (1941). The areas covered by these studies are relatively small, however, and much remains to be done before our knowledge of American dunes can compare with that of European dunes.

In the following paragraphs, the various criteria for interpreting dune history are outlined, progress in regional studies is reviewed, and some of the more important problems awaiting further study are noted. Many interesting questions as to morphology and dynamics of dune building, not directly related to the interpretation of dune history, are excluded from consideration.

Interpretation of wind direction.—The direction of former dune-building winds may be inferred from (1) dune morphology, (2) dune-sand bedding, or (3) the disposition of dunes or dune fields with respect to restricted sources of sand. Of these factors, dune morphology is the one most readily studied and, where sufficiently well defined and well preserved, is generally the one most nearly definitive as a basis for interpretation.

The correct interpretation of wind direction and other climatic factors from ancient dunes obviously depends on an adequate knowledge of the formation of dunes. In discussing this question, the various types may first be reviewed briefly. Empirically, two general classes of dunes may be distinguished: (1) those in bare, free sand, occurring mostly in true deserts, and (2) those wholly or partly covered with vegetation, and occurring in semi-arid to humid regions. Dunes of the first class include: (a) barchans, or crescent-shaped dunes with their convex side toward the wind; (b)

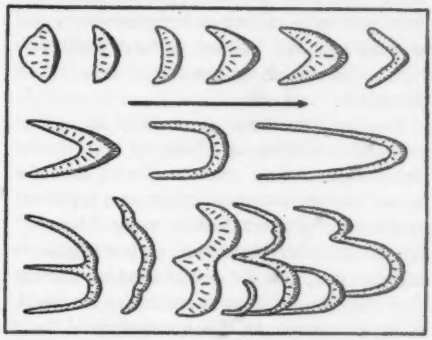

FIGURE 1.—DIAGRAMS SHOWING VARIETIES OF U-SHAPED AND RELATED DUNE FORMS WHICH COMMONLY ARE FOUND IN A STABILIZED CONDITION AND RECORD THE DIRECTION OF FORMER DUNE-BUILDING WINDS

Forms at bottom are composite; sketched from aerial photos and maps. Arrow indicates wind direction. Individual dunes range from a few hundred feet to a few thousand feet in length, ordinarily.

transverse dune ridges, extending at right angles to wind direction, and having a markedly asymmetric cross profile, with the steeper side facing away from the wind; (c) certain varieties of so-called longitudinal dunes, or sand ridges elongated parallel to wind direction; (d) wind-shadow dunes; and (e) various irregular forms. All these may be observed today in the active state; types (a) and (b) are particularly well known, and their migratory character and relations to wind direction are matters of common knowledge. Dunes of the above first class, however, do not enter directly into the interpretation of Pleistocene history unless they have been stabilized, or changed over into the second class, without loss of diagnostic features.

Dunes of the second class, those more or less stabilized, or covered with vegetation, generally show forms distinctively different from those of the first class. Particularly common are the forms described as parabolic, U-shaped, V-shaped, bow-shaped, horseshoe-shaped, etc. (Fig. 1), all gradational into one another and basically similar. These dunes

have the steeper slope on the side that is convex in ground plan and thus show the effect of winds from the opposite, or open side. Composite forms, produced by overlapping or fusion of unit forms, have rake-shaped or other varieties of outline in ground plan. Also there is a wide variety of irregular forms and of sand hills and hollows without distinctive form; these need be mentioned only to be dismissed.

In some situations, particularly in coastal areas, the relation of U-shaped and similar forms to associated dunes indicates that the former are of secondary origin and represent modification of antecedent forms by "blowout" action. In other situations, such evidence is not apparent, and the question as to whether they may be truly primary forms is raised. A correct answer to this question is of basic importance in the interpretation of past wind direction, and it was because of the conflicting answers proposed by different workers that controversy arose.

As early as 1894, Steenstrup described the "parabolic" type of dune and explained its development so as to imply that it is a primary form, conditioned by the presence of vegetation. Later, however, Solger, in a series of papers culminating in 1912, attempted to show that the ancient "bow-shaped" inland dunes of Germany were different from the "parabolic" dunes described by Steenstrup and others from coastal areas; he advanced the explanation that they originated as barchanlike dunes, which had their profiles overturned by a reversal of wind direction just before fixation. He thus pictured the dunes as being built primarily by periglacial anticyclonic winds from the east and subjected to secondary remodeling as the prevailing westerlies came into dominance. This view met with immediate opposition, which later was summarized and amplified by Högbom (1923), who showed the fallacy of Solger's reversal process and recognized that the present asymmetric profile of the dunes is a true indicator of former wind direction, but postulated that the dune forms developed from transverse dunes, in ways not clearly explained.

Still another interpretation was set forth by Enquist (1932), who pointed out Högbom's failure to consider adequately the role of vegetation in dune building, as clearly set forth by Steenstrup and others, and postulated that the observed dune forms must have developed as secondary modifications of antecedent longitudinal dunes built by periglacial winds. He thus returned part way to Solger's idea, although differing from Solger in his reasoning and in his conclusions as to the direction of the periglacial winds. Högbom (1932) and Hörner (1938) in turn refuted Enquist's main thesis, and Kádár (1938) in a detailed analysis of U-shaped dune development, reaffirmed Högbom's general conclusions, although differing in details of interpretation.

Studies by American workers (Melton, 1940; Hack, 1941) confirm the hypothesis that U-shaped dunes and related types are primary forms in some situations, and that continued presence of vegetation is essential for their development. The final stabilization of these dunes thus represents a shift in the balance between two factors present throughout the time of their growth, with vegetal growth gaining ascendency over wind action. It may be concluded that U-shaped dunes and the many variants of this form are built wholly by winds blowing from the open or concave side, do not necessarily imply antecedent dunes of other types, and are reliable indicators of the effective sand-moving winds of former dune-building times.

"Longitudinal" dunes are another type found in the stabilized condition. Their elongation has been assumed to represent the alignment of former winds, although leaving the direction along this alignment to be deduced from other evidences. The interpretation of this type of dune, however, is not without its problems. There is, first, a problem of distinguishing between actual longitudinal dunes and ancient transverse dunes which have lost distinguishing characteristics by weathering and eluvial processes. Högbom (1923, p. 213–216), for example, argued that the supposed longitudinal dunes of one Hungarian locality, although longitudinal with respect to present-day winds, were originally formed as transverse dunes when wind direction was approximately at right angles to that of today. The more detailed analysis of morphology now made possible by aerial photography (Madigan, 1936; Melton, 1940; Hack, 1941) should aid greatly in making

distinctions of this type. Another problem is the extent to which longitudinal dunes are actually built by unidirectional winds. Hack (1941) accepts the hypothesis that they are, but Bagnold (1941, Chapter 15) and Madigan (1946) attribute considerable importance to divergent winds. In the present state of knowledge, there is no reason for assuming that all dunes elongated parallel to wind direction were formed in the same way, or under the same conditions, and some caution in their interpretation seems to be in order.

True barchans and transverse dunes of the desert type have not been described in the stabilized condition, and the probabilty of their original form being maintained during the usually gradual encroachment of vegetation would seem to be small unless special conditions prevail. Neither these nor the other types of dunes not specifically discussed above are likely to enter into the problem of interpreting former wind direction.

The discussion thus far has been concerned mainly with dunes built by winds from one dominant direction, a condition realized or approached in many dune fields. Less has been written about those dunes built up by winds from varying directions. Högbom (1923, p. 234), however, suggested that the asymmetry of certain European dunes, in ground plan, was probably due to a shift in wind direction while they were being built. The same point was discussed at greater length by Louis (1929) and Kádár (1938). A more general discussion of the role played by divergent winds in dune building has been presented by Aufrère (1931; 1935) but has not yet been applied to the interpretation of dune history.

The interpretation of wind direction from dune-sand bedding alone is not without difficulties but may be the only course open where original dune form has been obliterated or severely modified by subsequent eolian or other erosion. The one safe generalization is that high-angle bedding is leeward. Where the dip is close to 30°, there is no question as to its significance. Where the only observable dips are considerably less than 30°, however, their meaning is less certain. I have observed dips lower than 15° on the leeward sides of small, dissected dunes. This probably occurs only on dunes of limited height, but the limit undoubtedly varies with local conditions and remains to be ascertained. The dividing line between high-angle and low-angle dips, in terms of their significance as indicators of windward and leeward bedding, likewise is not yet established. In any attempt to interpret dune bedding, it is important that true dip be distinguished from apparent dip, and that enough readings be made to give a representative picture for the dune as a whole.

The disposition of dunes with respect to source areas for sand is generally less definitive as an indicator of wind direction. Keilhack (1918), however, used it as one argument against Solger's hypothesis, and it may serve elsewhere to supplement other types of evidence or to provide some basis for interpretation where other evidences are lacking. Only where sand movement can be traced directly from a source area that is comparatively narrow in a cross-wind direction to the dune or dunes in question is a very definite figure obtainable. Where the source area is elongated in a cross-wind direction, as along many beaches, there may be a range of nearly 180° for possible wind direction. And where sand is blown from a vegetation-free area, such as a beach, to a vegetation-covered area, the process is to a certain degree irreversible, owing to the protective effect of the vegetation; the winds recorded by the sand accumulation may or may not be representative of the prevailing wind system.

Wherever wind direction is interpreted from dunes, it may be emphasized that it is the direction of the effective, sand-moving winds that is indicated, and that these may or may not correspond to the more persistent prevailing winds. The effectiveness of the wind depends both on ground conditions and on wind velocity. If velocity is the same, maximum effect is produced when the ground is dry and when vegetation affords least protection. Effectiveness is thus relative and varies with the seasons. And until wind velocity passes a certain critical value, there is no sand movement; beyond that value, the rate of sand movement "varies as the cube of the excess of wind velocity over and above the constant threshold value" (Bagnold, 1941, p. 69). Powerful storm winds of short duration thus may be far more effective than moderate winds of long duration; where the two do not coincide

in direction, the latter are not necessarily recorded in the dunes.

Dunes as indicators of former aridity.—The interpretation of former climatic environment from stabilized dunes is subject to certain limitations. What is indicated directly by ancient dunes is simply an available supply of reasonably dry sand exposed to winds of sufficient strength and persistence to move it in quantity. Weakening of the vegetal cover on sandy deposits by climatic desiccation is one important way in which a supply of sand can be made available. Other ways, however, include: (1) emergence of sandy sea floors by lowering of sea level; (2) production of barren areas by glacial recession more rapid than revegetation; (3) wave action on lake shores since abandoned; (4) stream action in sandy channels no longer occupied, or no longer characterized by a regimen such as to expose dry sandy flats during a part of the year; (5) soil desiccation due to lowering of water table by stream incision; and, (6) accidental destruction of vegetal cover by forest fires, prairie fires, etc. The first two factors have obvious geographic limits; within these limits, dunes of themselves do not necessarily indicate aridity. Where dune fields are of more than local extent, and do not correlate closely with any reasonably inferrable shore lines or stream channels of former times, or with modern streams that might once have flowed at a different level or had a different regimen owing to the influence of glaciation in their headwaters or other causes, the likelihood of factors (3–5) may be dismissed. Purely accidental factors such as fires probably would not result in dunes of very large size or extent. Thus, when detailed studies of particular areas rule out other possibilities, it may be concluded that stabilized dunes record the effects of a former interval of greater aridity in weakening the general vegetal cover. Where marshy ground or peat is associated with dunes (Solger, 1912; Keilhack, 1918), and particularly where it lies on the windward side (Högbom, 1923, p. 207), additional evidence of climatic change is provided, unless a rise in water table can be attributed to other causes (Korn, 1919; Högbom, 1923, p. 196).

The degree of aridity indicated by ancient dunes is another question. Solger (1912) and Enquist (1932), on the basis of differing but equally unwarranted assumptions as to original dune form, implied that the dunes of north Germany originated under desert conditions. Keilhack (1918) inferred a dry climate and a lack of vegetation. Högbom (1923, p. 235), after a consideration both of dune form and of other evidence, concluded only that the dunes south of the Baltic indicate a former dry interval. It is now certain that the U-shaped type of dune and its related forms develop only in the presence of some vegetation, and never in truly desert conditions. The possibility that the building of U-shaped dunes could have been preceded immediately by other types of dunes more representative of desert conditions, however, cannot be entirely dismissed. Conceivably such a generation of dunes could have been almost completely reworked into forms of a different type by the interaction of vegetation as aridity decreased. Obviously it would be unsound to postulate such a sequence of events without specific evidence.

Dunes as indicators of successive climatic fluctuations.—Where dune history has been complicated by more than one swing of the climatic pendulum, the evidence may be recorded either in the morphology or in the internal structure of the dunes. The effects of recurrent episodes of eolian activity on morphology may be analyzed in terms of an ideal cycle of development (Smith, 1940a), comprising eolian and eluvial phases. In the eolian phase, wind action is dominant, and dune forms are built up. Stabilization by vegetation introduces the eluvial phase, during which dune forms are gradually blurred and worn down by weathering and slope processes, through stages of youth, maturity, and old age, ending with obliteration of initial dune forms. The eluvial phase may be interrupted at any stage by renewal of wind attack, producing distinctive secondary forms of the "blowout" type; the resulting second-cycle eolian phase may in turn give way to stabilization and eluvial action. This sequence of events may be repeated many times, with many variations. The morphologic indications for such alternations, however, can be preserved in the same dune or dunes only when the intervals of eolian activity are successively shorter or less severe, else the earlier forms would be obliterated. There is reason for believing

nevertheless, that a given episode of wind action, especially if minor, does not necessarily affect all parts of a dune area equally—that some sections may be modified less than others, or even remain undisturbed.

The morphology of dunes is best studied with the aid of aerial photographs. In this way, the modification or transection of earlier dune forms by later blowout forms may be recognized, differences in degree of eluvial development may be distinguished, and successive phases of eolian activity differentiated. Where the dune topography is not too complex, and where the evidence from all parts of a sizable area fits into an orderly pattern, a sequence of past fluctuations in degree of aridity may be inferred (Melton, 1940; Smith, 1940a; Hack, 1941).

The evidence provided by the internal features of dunes supplements the evidence of morphology and may record phases of dune history that antedate the existing topographic forms. Studies of the internal features are best made in natural or artificial cuts through the ancient dune sands, but auger borings may be useful if actual cuts are lacing. Alternations between sand movement and other processes may be revealed by one or more of the following:

(1) Buried soil zones. Sayles' work in Bermuda (1931) represents a particularly effective application of this criterion, favored by the calcareous nature of the eolian sands. A succession of "fossil" dune-sand deposits and soils, believed to represent the greater part of the Pleistocene, was worked out. In Poland, buried humus layers associated with Mesolithic (Swiderian) artifacts have been studied (Clark, 1936) and correlated with the postglacial climatic succession. Buried soil horizons have been described also by Hack (1943) from Wyoming, by Judson (1946) from the Aleutians, and have been observed by the writer in central Kansas (Smith, 1938).

(2) Disconformities separating sands that contrast in color, degree of induration, or other characteristics. These relations have been used as a basis for interpretation by Huffington and Albritton (1941) and have been studied by the writer in central and southwestern Kansas (Smith, 1938; 1940a).

(3) Interbedding of dune sand with peat, lacustrine sediments, or other deposits such as might have been laid down in interdune depressions or on surfaces immediately adjacent to dunes, during intervals of stabilization.

Dating of ancient dunes.—Where dune studies point definitely to one or more climatic changes, dating is the final step in interpretation. Unless the dune chronology can be correlated, at one or more points in time, with the standard Pleistocene chronology, it is left dangling in time and is of uncertain historical significance. Direct evidence of age may be provided by one or more of the following:

(1) Relation to glacial deposits or to stream terraces, lake stages, or sea-level changes which can be correlated with the standard chronology. This type of evidence, where, available, is particularly useful in determining a lower limit for age. Examples are given by Högbom (1923).

(2) Relation to peat bogs or other deposits dated by pollen analysis. This method of approach is discussed by Wildvang (1935) and Dewers (1935).

(3) Presence of datable fossils in the dune sand or in associated sedimentary deposits (Evans and Meade, 1945).

(4) Presence of datable artifacts. Although Högbom attached considerable importance to the presence of artifacts in European dunes (1923, p. 202), subsequent archeological studies have led to the conclusion that artifacts are of very limited value as "guide fossils" in the Old World.[2] In North America, the archeological record does not extend as far backs as in Europe, and has been less intensively studied. At present, strictly geologic critera appear more significant than artifacts for dating dunes. (Cf. Hack, 1943.) The presence of Folsom or Yuma cultural material, however, does seem to point to some degree of antiquity, and with further progress in correlating artifacts with geologic chronology the value of the artifacts as indicators of age may increase.

Where the above direct evidences as to age are not found, to the following may furnish indirect and less definite evidence:

(1) Weathering and soil profile development. Both Solger (1912) and Keilhack (1918) used

[2] H. L. Movius, Jr., personal communication; see also paper by Movius in this series.

this criterion in postulating a considerable degree of antiquity for the German inland dunes. Differences in degree of weathering and soil development were also used by Keilhack (1914) in distinguishing dunes of different ages, and were elaborated upon by Dechend (1937). In this country, Sellards *et al.* (1923) employed a similar approach in dealing with comparatively recent dunes. Unless comparisons can be made with weathering on other types of sandy deposits of similar composition, under similar climatic conditions, that are datable by other methods, only the most general inferences as to age can be drawn from weathering phenomena.

(2) Stage of morphologic development. Stage of development in the eluvial phase of the dune cycle offers a possible basis for estimating age. A basis for comparison must first be obtained, however, from studies on the morphology of dunes of different ages that have been more definitely dated by other criteria.

These two indirect methods of approach are complementary and, of course, are best used in conjunction. Their future value will depend on the discovery and study of critical localities where they may be correlated with direct evidences of age.

Regional studies.—Högbom's monograph of 1923 remains the most comprehensive study of European dunes. His main conclusions were as follows: (1) Fennoscandian dunes are dated as latest glacial (Finiglacial) by relations to fluvioglacial deposits and to sea levels, and were formed by periglacial winds blowing outward from the ice; (2) there is no evidence that periglacial winds played any part in developing the dune forms observed in Germany and Poland, although the possibility of earlier sand drifting by such winds is admitted; (3) the dunes are unrelated to the loess deposits of central Europe and are believed to be younger; (4) the orientation of the German dunes is somewhat divergent from that which would be expected of dunes built by the wind system now prevailing; (4) archaeological evidence indicates that the dunes of Germany and Poland are not younger than Neolithic, and climatological deduction suggests a Finiglacial or early postglacial age; (6) the dunes south of the Baltic indicate a former drier interval.

In North America, dune studies have been fewer and more widely separated than in Europe. In the Great Lakes region, Cressey (1928), Stevenson (1931), Bergquist (1936), Scott and Dow (1937), and Dow (1938) have contributed to the historical geology of the shore dunes, particularly to their relation to lake stages. The writer's studies in the same area (1940b) indicate further that the ancient dunes were formed by winds similar in direction to those now active, and were not "periglacial".

A dune area near Minneapolis was described by Cooper in 1935, and compared with dune areas in Europe. The dunes are of bow-shaped and related forms and indicate southwesterly winds. They were dated as postglacial and were believed to have resulted from soil desiccation due to lowering of the water table by downcutting of streams. The possibility of a former interval of drier climate is admitted, but only as a contributing factor. The argument here, however, is open to question. Cooper admits that there is evidence of an appreciable lapse of time between downcutting and the beginning of sand drift, which would be difficult to explain if stream incision alone was the effective cause. Furthermore, it is not clear why the dune areas should have become stabilized unless the climate later became less favorable for wind action, other conditions remaining the same. The reader may prefer to consider the dunes themselves as evidence of a former drier interval, with stream incision only as a contributing factor. Cooper himself could not entirely dismiss the climatic factor, and stated (p. 104), "Assuming that climate was a contributing cause, it is natural to assign the process to a dry period in postglacial time, and if there were two of these, to the earlier one."

In southern High Plains, Melton (1940) distinguished three series of dunes, on the basis of comparative morphology. Series I comprises all active and recently active dunes, dominantly secondary form. Series II comprises somewhat older stabilized dunes including primary forms, and indicating a wind direction only slightly different from that of the present. Series III is the oldest, comprises primary U-shaped dunes of distinctive form, and is unique in indicating a wind direction nearly transverse to that recorded in the younger series. Dunes of Series II are correlated with eolian deposits bordering the highest stand of lake Estancia, believed

by Antevs to date back about 15,000 years. The full significance of Melton's findings probably will not be clear until more is learned of their broader regional setting.

Other studies in the southern High Plains have been made by Huffington and Albritton (1941), Hefley and Sidwell (1945), and Evans and Meade (1945). Evans and Meade report dune sands ranging probably from early to late Pleistocene time.

In the central High Plains, dune topography is more complex than in regions to the north and to the south, and the sequence of events is less clearly recorded. My studies indicate, however, that several generations of dunes are present, and that the major dune areas, totaling hundreds of square miles, are predominantly stabilized, could not have formed under present climatic conditions, and must have originated during one or more past intervals of greater aridity (Smith, 1940a). No direct evidence as to the age of the stabilized dunes has yet been found.

In the Navajo country in northeastern Arizona, Hack (1941) has described an extensive dune field containing longitudinal, transverse, and "parabolic" forms. He found the relation of active to stabilized dunes indicative of a former drier or windier interval separated from the present by a less arid interval. The former episode of dune building was correlated with valley-fill deposits and tentatively assigned to the postglacial "climatic optimum", or warmth maximum.

Problems.—At present, the general principles of dune formation are fairly well understood, and their application to the interpretation of late Pleistocene history has been demonstrated in Europe. The problems awaiting further investigation fall into three main classes.

(1) More detailed study of the morphology and origin of dunes. Although the main types of dunes are now known, many of the varieties remain to be more carefully distinguished, more clearly defined, and more closely correlated with conditions of genesis. The "longitudinal" type of dune in particular needs further study and probably will be found to include forms which are morphologically distinct and genetically diverse. Studies directed toward these ends need to be carried out in areas where dunes are now being built, so that the relations of form to vegetation, sand supply, wind velocity and direction, and other factors can be observed. Detailed meteorologic observations are particularly needful. Is wind velocity an important factor in determining dune form, as postulated by Melton (1940) and others? How important are alternating winds of different velocities from different directions in the development of certain longitudinal dunes? These and related questions cannot be answered from the generalized data available from U.S. Weather Bureau publications, in which winds of different velocities are lumped together.

(2) More definite formulation of the criterion value of features in stabilized dunes, for the interpretation of age and past climatic changes. Studies of the type mentioned in the preceding paragraph will, of course, contribute here, but additional studies on the significance of dune-sand bedding, and on soil development on dated dunes of different ages, under different environmental conditions, are desirable. Collaboration between geologists and soil scientists should be most helpful.

(3) Application of established principles and methods to regional studies. Extensive dune areas in North America, particularly in the Great Plains, have not yet been described. Investigations on form and orientation of dunes in these areas, and of their relation to loess, alluvial terraces, and other types of deposits, should contribute substantially to our knowledge of late Pleistocene history in the regions concerned, and should help provide a basis for the reconstruction of past wind systems and other climatic conditions. Here also collaboration between geology and soil science should be fruitful.

Disseminated Eolian Sand

A novel method of approach to the study of periglacial wind action was described by Cailleux in 1942, and reviewed at length by Wright in 1946. This method is based on eolian sands which are not concentrated in dune form, but occur disseminated in other types of deposits. The percentages of eolian sand grains (as indicated by frosting) in the coarse sand fractions from some 3000 samples of European Pleistocene sediments were determined, plotted, and contoured. Percentage of frosted grains was

used as a criterion of the intensity of wind action, and on this basis the zone of periglacial wind action was outlined and its implications analyzed.

Ventifacts

Ventifacts, or sand-blasted stones (Bryan, 1931), are significant in the study of Pleistocene geology where they are buried in superficial deposits, and where they occur at the surface in areas no longer characterized by sand blasting. They are suggestive as to the former intensity of wind action, and the former prevalence of environmental conditions suitable therefor, but ordinarily give no indication of wind direction.

The association of ventifacts with areas bordering the present-day glacier of Greenland was described by Hobbs (1931) and Flint (1948). Analogous conditions have been inferred from the occurrence of "fossil" ventifacts in continental glacial depostis, as recorded by Cailleux (1942) in Europe, and by Powers (1936), Thiesmeyer and Digman (1942), Mather *et al.* (1942), and Thiesmeyer (1942), in the United States. The occurrence of ventifacts on the Iowan drift also has been discussed by Leverett (1942). In areas near former valley glaciers, ancient ventifacts have been described by Blackwelder (1929), Powers (1936), and Bryan and Ray (1940, p. 22, 26, 30). The evidence of ventifacts, together with that of the disseminated eolian sands analyzed by Cailleux (1942), point to the existence of conditions favorable for vigorous wind action in former periglacial zones. Only where the sand blasting is found on bedrock ledges, however, or on boulders of such size and position as to have escaped movement, is evidence of past wind direction provided.

The occurrence of ventifacts scattered through surficial soil materials has been noted by Bastin and Cailleux (1941) in France, and by Bryan (1932), Denny (1936), and Mather and others (1942) in this country. This relationship is regarded as indicative of soil churning by intensified frost action under periglacial conditions.

Weathered ventifacts and wind-eroded surfaces above ground in areas remote from former glaciers have been described by Denny (1941) and by Bryan and Albritton (1942). Such occurrences point to past climatic conditions more favorable for wind erosion than those of the present, and supplement other types of evidence relating to such conditions.

The problems relating to ventifacts are primarily those of distribution, both areal and stratigraphic, and of interpretation in terms of local historical significance.

Deflation Basins

The part played by the wind in excavating shallow basins has been discussed by Gilbert (1895), Berkey and Morris (1927), Blackwelder (1931), and many others. More recently, Evans and Meade (1945) have argued that deflation was a major factor in the development of numerous inclosed basins in the High Plains section of Texas. These basins are of particular significance for their record of Pleistocene events. Deepening of the basins was interpreted as a result of deflation during recurrent times of greater aridity, while lateral expansion was effected by wave erosion, gulleying, and other processes during intervening times of greater humidity. Sediments deposited when the basins contained lakes provide a partial record of events dating back to early Pleistocene time.

Loess

The present status of studies on loess has been reviewed in ample detail by Zeuner (1945) with reference to European areas, and by Flint (1947, p. 175–187, 465–467) on a world-wide basis. Here it is desirable only to note certain of the problems:

(1) Distinction between true eolian loess and other loesslike deposits. This problem is suggested by Russell's challenge (1944) to the hypothesis of eolian deposition of loess in the lower Mississippi Valley. Russell invoked instead a process termed "loessification," involving derivation by weathering of parent material (clayey deposits on Pleistocene terraces), and sorting through downslope creep. The application of this hypothesis to other regions was implied. Criticism of these conclusions was quick to follow. Both Holmes (1944) and Thwaites (1944) pointed out flaws in the argument, and the latter argued specifically against extension of Russell's hypothesis to loess in the upper Mississippi Valley. More could be said, particularly in regard to Russell's failure to consider petrographic data relevant to the origi-

of the loess. However, a need for more critical observation on loesslike deposits, and for more careful distinction between loess deposited directly from the atmosphere, and that reworked by creep or running water does seem to be suggested.

(2) Distribution of the loess. In the upper Mississippi Valley, the areal distribution of the loess is well known. Variations in the thickness of the loess, however, have been mapped in only one State, Illinois (Smith, 1942). Smith's study is of particular interest for its quantitative approach and provides a model for studies in other areas. Texture and thickness of the loess were found to vary directly with distance from the river bluffs, and carbonate content was found to decrease as the loess thins.

In the Great Plains, studies on loess are less advanced than in the upper Mississippi Valley. The area extent of the loess has not yet been mapped with any degree of completeness, and the age of the loess is yet to be established at many places. A beginning has been made, however, in Nebraska and Kansas. Condra, Reed, and Gordon (1947) have summarized conclusions on the Nebraska loess, although the detailed data on which these conclusions rest have not yet been published. Correlations between Kansas and Nebraska have been postulated by Frye and Fent (1947). Much remains to be done in extending such studies southward and westward.

In other parts of North America, with the exception of the Pacific Northwest in the United States, still less is known about the distribution of loess.

(3) Source areas for particular loess deposits. For many areas, the relative importance of the following types of source areas remains to be determined: (a) glacial outwash; (b) bare ground due to the effect of periglacial climate in depleting vegetation, or to deglaciation more rapid than revegetation; (c) desert areas, in general; and (d) dune fields. Studies in thickness variations and textural gradations of the loess, as noted under (2) above, will contribute to the solution of this type of problem.

Volcanic Ash

Volcanic ash is mentioned here in the interest of completeness. It is important mainly as a horizon marker in aiding the correlation of other types of Pleistocene deposits. It has no climatic significance except to indicate, by its distribution with respect to particular eruptive centers, the direction of the winds blowing at the immediate time of eruption.

The extensive distribution of individual ash falls is well known from historic eruptions, such as that of Tambora, in 1815, and of Katmai, in 1912. Ancient ash falls having a correspondingly wide distribution have played a part in the interpretation of the North Atlantic deep-sea cores (Bradley *et al.*, 1942) and of the Pleistocene sequence in the Great Plains. In the latter area, the stratigraphic significance of a Pleistocene volcanic ash horizon was studied on a regional basis by Leonard (1947) and Frye (Frye *et al.*, 1948).

Frost Action and Related Phenomena

Introduction

Features produced by intense frost action and related effects are significant in the interpretation of Pleistocene history where they occur as "fossil" forms, in places no longer having the type of climatic environment required to produce them. In such situations, they provide evidence of past climatic conditions characterized by temperatures lower than at present, with differences in the amount and seasonal distribution of precipitation as a possible additional factor. Recognition of the phenomena in question rests on a critical discrimination between both landforms and superficial deposits, which are now actively in process of formation, and those which are now inactive, and subject to processes of modification and decay. Other conditions remaining the same, the latter features indicate changes in process related to changes in climate. Comparison of those features with corresponding ones now being formed in colder regions provides a basis for interpreting the type of climate involved. Studies in this field have been in progress more than half a century and have given rise to the concept of a "periglacial" zone of indefinite width, marginal to continental ice sheets, and characterized by various types of intensified frost phenomena, as well as by the eolian effects discussed in the preceding section of this report.

The writer here reviews the historical development of studies on frost phenomena, discusses briefly each of the principal types of features significant for the interpretation of former climatic conditions, considers the progress made in regional studies, and notes the more important problems remaining.

Historical Review

European work.—The present status of studies on frost phenomena is best viewed in the light of its historical development. The early history had its setting in England.[1] First was the recognition, more than a century ago, of anomalous deposits of heterogeneous, unsorted, nonstratified materials of local derivation, variously referred to as "Head," "Warp," "Coombe Rock,", "Rubble Drift," etc. This material was found to be widespread in nonglaciated areas, and gradually various workers realized that it is unrelated to any processes of transportation now observable in those areas. The idea of accumulation under conditions different from those of the present naturally followed, and these conditions were pictured as involving one or more manifestations of lowered temperature—frozen ground, frost action, and effects of a thicker and more persistent snow cover. Although one writer appealed to uplift of the land to account for the cold, the climatic conditions associated with glaciation of near-by areas came to be generally accepted as the effective factor. By 1894, sufficient work had been done to permit a regional summary by Geikie, who reaffirmed the glacial dating of the rubble deposits and analyzed the probable conditions under which they were formed.

In 1896, Blanckenhorn reviewed the English work and pointed out applications to German areas. He showed that certain supposed morainal deposits were better explained as formed in the same way as the British "warp" and better classed as "pseudomoraine."

The next important contribution (Andersson, 1906) formulated the concept of solifluction; on the basis of observations in the Arctic, Andersson applied the concept to the interpretation of the "stone rivers" of the Falkland Islands. He concluded that these features were "fossil" products of solifluction, formed under a former "subglacial" climate. He also briefly surveyed both modern and ancient occurrences of solifluction in other parts of the world.

In 1909, Lozinski introduced the term "periglacial" as more appropriate than "subglacial," but failed to define the term explicitly. In 1912, Lozinski discussed periglacial phenomena at greater length. He emphasized the importance of frost weathering under periglacial climatic conditions for the production of various block accumulations, but differed from Andersson in giving scant consideration to movement of the weathered material.

In 1910, the International Geological Congress excursion to Spitsbergen gave many European geologists their first opportunity to observe arctic frost phenomena, and provided a stimulus for the study of comparable phenomena, in Europe.

Högbom's monographic treatment of frost action (1914) marked a milestone in the progress of studies on these phenomena and remains a standard reference in this field. In Högbom's work, based largely on his observations in Spitsbergen, the occurrence and significance of perennially frozen ground was discussed, and a wide range of frost-induced phenomena was described and analyzed in detail. A regional summary of the occurrences of both modern and "fossil" flow-earth phenomena was included.

In the years ensuing studies by Salamon (1917), Meyer-Harrassowitz (1918), and others led to widespread recognition of periglacial frost phenomena in northern Europe. In 1925, Kessler presented a comprehensive summary of work on periglacial phenomena up to that time. This work may be regarded as a second milestone in the progress of these studies, and undoubtedly provided a strong stimulus to further investigations. Thereafter, the literature became voluminous, a wide range of phenomena was recognized as periglacial, and the areal occurrence of these phenomena was outlined.

Although the periglacial concept came into wide acceptance (Woldstedt, 1929), skepticism on some points was voiced by a few geologists, of whom W. Penck (1924) was perhaps the most influential. Penck questioned whether the block

[1] An excellent review of the development of British thought on this subject has been presented by Dines and others (1940).

fields, generally attributed to periglacial processes, are now stabilized, as supposed, and whether frost weathering was particularly essential to their formation. He cited examples of blocky accumulations in regions where effective frost action could not reasonably be inferred, even during glacial stages. He concluded that lithology rather than climate is the important factor. Schott (1931) reached similar conclusions from studies in the German uplands. Büdel (1937) critically evaluated the conflicting viewpoints, on the basis of studies in the Erzgebirge and Riesengebirge of Germany. He found a widespread mantle of rubble which, in contrast to former vigorous movement, was shown to be completely immobile at present, within certain limits of slope; moreover, decisive proof that stabilization had continued throughout postglacial time was adduced. Present-day activity of rubble was found only on a minor scale, in places particularly favorable due to steep slopes or high elevation. The sweeping generalizations of Penck and Schott were thus refuted. In the meantime, other workers discovered positive evidence of the former existence of perennially frozen ground in the periglacial belt, and so confirmed deductions from mass-movement phenomena as to the severity of the periglacial climate.

Subsequent to Büdel's work, the various aspects of frost action, both modern and ancient, have been elaborated upon by many European workers. Of particular interest was Troll's (1944) world-wide survey of modern frost phenomena, including a climatic classification of the typical surface forms involved. Other papers will be referred to under appropriate headings in the following pages.

Russian studies on frost phenomena have been concerned mainly with regions of perennially frozen subsoil. Some of the earlier literature was summarized by Leffingwell (1919), and a more general summary was provided by Muller (1945).

North American studies.—In North America, progress in the study of frost phenomena, both modern and periglacial, lagged far behind that in Europe. As early as 1881, however, Kerr visualized the far-reaching effects of climatic changes associated with glacial stages and postulated that the character and disposition of certain superficial deposits in the southern States were a product of frost action during the ice age. T. C. Chamberlin later (1897) remarked, "It must be remembered that as a result of the excessive superficial thawing and freezing incident to glacial-border conditions, the facilities for landslides, bodily creeps, and similar modes of movement reached an extraordinary degree of development." Neither of these ideas, however, was productive of further investigation.

In 1900, Matthes introduced the concept of ***nivation*** and showed its importance as a geologic process under alpine conditions. Subsequent American studies for some 30 years were confined to arctic and subarctic regions. The work of Leffingwell (1915; 1919) on ground-ice wedges and associated phenomena was noteworthy and has been widely quoted. Important contributions on solifluction and related phenomena were made also by Eakin (1916), Ekblaw (1918), and Capps (1919).

In 1928, Bryan introduced Kessler's (1925) work to American geologists, thus directing attention to the problems of periglacial phenomena, and preparing the way for study of these phenomena in the United States. Soon thereafter, Taber (1929; 1930) presented experimental studies of fundamental importance for the understanding of frost phenomena. In subsequent years, periglacial phenomena were described from various localities in the United States by Eakin (1932), Antevs (1932), Bryan (1932), Denny (1936; 1938), Smith (1936; 1941; Smith and Smith, 1945), Bryan and Ray (1940), Eargle (1940; *see also* Bryan, 1940), Sharp (1942a), and Peltier (1945). Modern frost phenomena also, mainly in mountainous areas, were described by Antevs (1932), Russell (1933), Behre (1933; *see also* Bryan, 1934), Nichols and Nichols (1936), Denny (1940), Sharp (1942b), Rozanski (1943), and Butler and Ray (1946).

In Arctic regions, studies of modern frost action have been made by Bretz (1935), Sharp (1942c), Taber (1943), Washburn (1947), and Flint (1948). An extensive research program is now being carried on in the U. S. Geological Survey, but only one of the resulting studies has yet been published (Wallace, 1948).

Types of Features Interpreted as Periglacial

General statement.—Intense frost action involves: (1) accelerated mechanical weathering; (2) growth of ground ice; (3) volume changes

in surficial deposits; (4) differential, nonprogressive movement of soil materials, leading to rude sorting under certain conditions; and (5) mass movement of detritus on slopes. These effects are combined in various ways to produce distinctive landforms and surficial deposits unlike those developed by other geologic processes. Where these features are of such composition and/or localization as to escape destruction by weathering and erosion, they may persist for long intervals of time, and bear witness of the past climatic conditions which governed their formation. The principal types of features interpreted to have this indicator value are briefly discussed below. No very detailed descriptions or explanations of the various features are purposed, but reference is made to other papers in which these matters are covered at greater length. The order of listing is roughly that of relative interest, as based on both criterion value and frequency of occurrence.

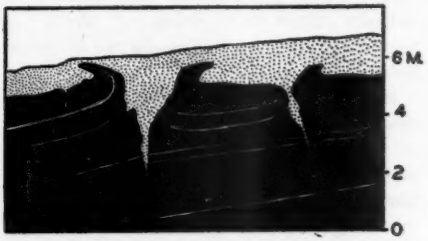

FIGURE 2.—DIAGRAM SHOWING LOAM-FILLED CASTS OF ANCIENT GROUND-ICE WEDGES IN TRIASSIC ARGILLACEOUS BEDS SOUTH OF GÖTTINGEN, GERMANY

Drawn from photo by Lotze (1932, p. 72). vertical scale approximate.

Ground-ice wedges.—Wedge-shaped segregations of ground ice have been described from arctic regions by Leffingwell (1915; 1919), and Taber (1943). Frost cracks without visible ice have been noted also by Paterson (1940) and Washburn (1947), and the geographic distribution of the latter has been summarized by Troll (1944). The ice wedges range up to about 8 feet in width and have been observed to depths of 30 feet, which is believed to be only a minimum figure for their actual depth. The ground surface associated with ice wedges and frost cracks is commonly marked by distinctive rectangular or polygonal patterns, with unit cells several tens of feet in diameter. According to Leffingwell, the ice wedges formed by passive filling of frost cracks with ice and grew by successive additions of ice as the cracks were reopened seasonally through successive years. Taber, however, concluded that the growth of the ice mass itself

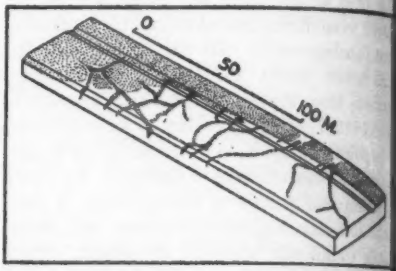

FIGURE 3.—ISOMETRIC BLOCK DIAGRAM SHOWING NETWORK PATTERN OF LOESS-FILLED CASTS OF ANCIENT GROUND-ICE WEDGES IN JURASSIC BEDS

On grade of Göttingen-Kassel highway, in Germany; after Selzer (1936, p. 282).

exerted an expansive force. Both hypotheses require preservation of the ice during the season of thawing, a requirement met only in regions of perennially frozen ground.

"Fossil ground-ice wedges,"[4] or cracks filled with clastic materials (Fig. 2), have been described from European areas by Kessler (1925, p. 101–105), Lotze (1932), Soergel (1932; 1936), Selzer (1936), Paterson (1940), Bastin and Cailleux (1941), Weinberger (1944), and others, and from Alaska by Taber (1943, p. 1493, Pl. 10). These features are found in sand and gravel as well as in finer-grained materials. At some places polygonal ground plan is revealed (Fig. 3). The filling may consist in part of material slumped from the sides, but commonly includes some new material, such as loess. A special case of eolian sand as the filling material was reported by Bastin and Cailleux (1941), thus bringing together the evidences for two different types of periglacial phenomena. In many occurrences the bedding in the sediment adjoinging the crack is more or less distorted along the wall of the crack.

The only type of crack which might possibly be confused with these structures is that pro

[4] Variously referred to as "frostrisse," "frost spalten," "diluviale eiskeile," "lösskeile," and "lehmkeile."

duced by desiccation, which in rare instances reaches depths of 10 feet or more (Shrock, 1948, p. 195, Fig. 159). Soergel first interpreted the filled cracks in Germany as a result of desiccation, but later (1932) rejected that explanation in favor of ground-ice origin. Desiccation cracks differ from ice-wedge fissures in being restricted to argillaceous sediments, in being narrow in proportion to depth, in the absence of marginal distortion of the wall rock, and in greater regularity of form.

The casts of ancient ground-ice wedges are considered one of the most positive evidences of former periglacial conditions comparable with those of present-day subarctic and arctic regions. They could have formed only in association with perennially frozen ground, which, according to Taber (1943), requires a mean annual temperature not higher than about 26°F. Poser (1947a; 1947b) relied on this criterion to a considerable extent in reconstructing periglacial climatic conditions in Europe during the Würm glacial stage.

Solifluction deposits.—The term "solifluction" has been used with different meanings by different writers; it is used here as a general term to denote progressive downslope movement of presumably saturated detrital material under the action of gravity, probably working in conjunction with frost heave in most instances. This process has been described from Arctic regions by Andersson (1906), Högbom (1914), Eakin (1916), Ekblaw (1918), Capps (1919), Poser (1932), Bretz (1935), Paterson (1940), Washburn (1947), and others. Continued saturation is generally considered a necessary condition, with moisture supplied by gradual melting of snow and/or interstitial ground ice. Taber (1943) has pointed out that, where the frozen ground contains actual segregations of ground ice, the volume of water liberated by thawing may be excessive, producing what might be considered a state of supersaturation, particularly conducive to flowage. The part played by perennially frozen subsoil in maintaining saturation by preventing loss of water by downward seepage has been emphasized by several observers.

Although solifluction has been known in a general way for a long time, the results have not yet been described in adequate detail. More attention has been given to the surface form than to the internal composition of the resulting deposits, and it is the latter which enters into interpretation of periglacial conditions. It has been observed, however, that blocks and coarse detritus are commonly carried along by the muddy mass, and that movement occurs on slopes of comparatively moderate gradient. This provides some basis for comparison with ancient deposits.

Recognition of ancient solifluction deposits began, and essentially correct deductions as to their origin were made, before the process itself had been studied under present-day conditions (Geikie, 1894). It is now generally recognized that such deposits are widely distributed in the unglaciated areas of northern Europe, and representative descriptions may be found in the works of Kessler (1925), Nordmann (1928), Breuil (1934), Dines *et al.* (1940), and others referred to in the section on "Block fields."

The solifluction deposits are characterized by their nonstratified, unsorted, heterogeneous, till-like appearance, by drag effects on the substrata, by contortions and other irregularities in the basal zones of the deposits themselves, and by present immobility. Unless the proportion of blocky material is large, the surface expression is not very distinctive, and the deposits are best studied where exposed by erosion or by artificial excavation. True solifluction deposits are to be distinguished from mudflow deposits formed more rapidly under a different set of conditions (Sharpe, 1938, Ch. 4).

The presence of striated blocks in solifluction deposits has been reported by Breuil (1934) and by Büdel (1937, p. 19). This suggests that some at least of the striated cobbles described by Wentworth (1928) from the Southern States may have acquired their striations as a result of transportation by solifluction.

According to Breuil (1934) and Wernert (1938), solifluction deposits play an important part in the Pleistocene stratigraphy of northern France. Breuil described a succession of solifluction layers separated by loess and fluvial deposits, and correlated the solifluction deposits with successive glacial stages, partly on the basis of associated vertebrate faunas and archeologic material.

The climatic significance of solifluction deposits is discussed below in conjunction with that of the block fields.

Block fields and related features.—Surficial concentrations of blocks or boulders (Pl. 1) have been referred to variously as "block fields," "boulder fields," "felsenmeere," "blockmeere," and "blockfelder." Where such accumulations extend along valley bottoms, the terms, "stone rivers," "rock streams," "blockströme," etc., have been used. Relict features of this general type have been described from the Falkland Islands by Andersson (1906), from various upland areas in northern Europe (Lozinski, 1912; Salamon, 1917; Meyer-Harrassowitz, 1918; Quiring, 1928; Fourmarier, 1933; Büdel, 1937; and others), and from scattered areas in the United States (Smith, 1941; Smith and Smith, 1945; Peltier, 1945).

Theoretically, block fields could be produced either by mechanical weathering in place, alone, or by mechanical weathering plus downslope movement. Lozinski (1912) emphasized the former, and present-day examples of the process have been noted by Högbom (1914) and others. Only where the block fields occur on flat surfaces or on topographic highs, however, can the factor of transportation be dismissed without adducing specific proof. A majority of the occurrences described lie on sloping ground and are believed to have involved some transportation of the block material. Where critical studies have been made, specific evidence of transportation has been found in one or more or the following relationships: (1) content of exotic block material traceable to restricted source areas on the upslope side; (2) downslope bending or stretching of beds or structural lines in the subjacent rock; and (3) inversion or interruption of the normal soil profile, as by occurrence of less weathered rock overlying more deeply weathered rock. The block fields thus represent a special facies of solifluction deposits and are distinguished on the purely superficial basis of conspicuously blocky or bouldery surface expression. In many places, the latter aspect appears to have been accentuated locally by washing away of interstitial fine material originally present.

Block fields obviously serve as indicators of former climatic conditions only where they are now immobile and no longer in process of formation. Evidence of stabilization may be found in: (1) growth of vegetation, particularly trees, on or immediately adjacent to the blocky area, without disturbance; (2) secondary weathering effects on the blocks, such as to indicate breakdown in place, without disturbance or appreciable differential movement of the resulting fragmental material; (3) beginnings of soil profile development without interference; (4) presence of overlying deposits of other types in an undisturbed condition; and (5) indications that the work of running water has regained its status as the main process of erosion, after an episode of interruption by rubble accumulation. From such evidences Büdel (1937) demonstrated that block accumulations in the Erzgebirge and Riesengebirge areas of Germany are now immobile on slopes up to 17°. By finding a complete postglacial pollen sequence, beginning with a subarctic birch-pine flora, in undisturbed bog deposits overlapping the rubble mantle, he proved further that stabilization had prevailed throughout postglacial time and that the mass movement of the rubble was truly a periglacial phenomenon.

Assignment of solifluction deposits to periglacial origin still leaves the question as to just what type of climate was responsible for their formation. Paterson (1940) expressed doubt as to whether solifluction indicates an arctic type of climate, unless supplemented by other more definitive types of evidence; he pointed out that the primary requisite for solifluction is saturation, and that this condition may be found under special conditions in other than frigid environments. Washburn (1947) reached similar conclusions. It is undoubtedly true that simple soil flow or saturated creep can occur under a wide variety of conditions, ranging from perennially frozen subsoil through seasonally frozen ground to unfrozen ground with impervious substrata. There is no reason for assuming, however, that periglacial mass movement took place by simple flowage alone. Indeed, it is difficult to visualize the transportation of coarse rubble in large volume for distances of more than 2 kilometers, and on slopes as low as 2°, as reported by Büdel, by mere soil flowage alone, particularly where this material is now stable on slopes up to 17°. If powerful frost heaving such as would occur under conditions of perennially frozen subsoil, be admitted as a complementary factor, the process of movement becomes more intelligible. (Cf. Eakin, 1916; Kessler, 1925, p. 108–110.) Unfortunately, ex-

iting knowledge of present-day mass movement under arctic conditions is too superficial to throw much light on this matter. It may be concluded that a stabilized mantle of coarse rubble or blocks on low gradients, unless definitely attributable to special local conditions, is indicative of a former colder climate, and strongly suggestive of a once perennially frozen subsoil. Where "solifluction" deposits are particularly well developed and widespread, it may be inferred further that the periglacial climate was of a relatively humid type (Zeuner, 1937).

Involutions in unconsolidated sediments.—Highly irregular, aimlessly contorted, interpenetrating structures (Fig. 4) in Pleistocene sediments have been variously referred to as "involutions," "cryoturbations," "würgeböden," "taschenböden," and "brodelböden."[5] Structures of this type have been described from Germany (Keilhack, 1927; Bahr, 1932; Steeger, 1944), Denmark (Nørvang, 1946), Holland (Edelman *et al*, 1936), and from this country (Denny, 1936; Sharp, 1942a). These structures are found in flat-lying sediments and are characterized by random orientation and lack of lateral continuity, in ground plan; no progressive movement is involved in their formation. They are thus distinguished from the drag structures produced by solifluction and from drag and flowage structures produced by other processes not related to frost action (Shrock, 1948, 156–160, 258–280).

Sharp gave detailed descriptions of involutions and discussed the question of origin at some length. He concluded that the involutions were formed by intense differential freezing and thawing, together with the growth and melting of bodies of ground ice. Nørvang, in discussing more or less similar features, postulated buried soil polygons (described below). Since these features have no definite surface expression insofar as known, no direct evidence as to their origin has been observed in arctic regions. It is generally agreed, however, that they could have been formed only in association with perennially frozen ground, and thus provide good evidence of former frigid periglacial conditions. Poser (1947a) used these features as one criterion in reconstructing periglacial climate in Europe during the last glacial stage.

Stone rings, stone stripes, and related features.[6] Stone rings or polygons, commonly joined together in a network pattern (Pl. 1), are typical features of flatish surfaces in many arctic and alpine regions. As the slope increases, they grade through elongate or garland-shaped forms to stone stripes. The literature on these features is voluminous, and probably more papers have been written about them than about any other product of frost action. Representative studies are those of Högbom (1914), Eakin (1916), Huxley and Odell (1924), Elton (1927), Poser (1931), Antevs (1932), Steche (1933), Sharp (1942c), and Orvin (1943). A regional summary of occurrences now in the active state, together with a climatic classification, was presented by Troll in 1944.

FIGURE. 4.—"BRODELBODEN" OR INVOLUTIONS IN PLEISTOCENE SEDIMENTS

Drawn from photo by Keilhack (1927, opp. p. 364).

Stone rings are evidently formed by the sorting effects of frost action, but the details of the process are not yet clearly understood. Sharp (1942c) reviews the various hypotheses, but none seems adequate to account for all observed characteristics of the nets in general. Stone stripes and intermediate forms are believed to result from the interaction of solifluction with the process of stone-ring development.

"Fossil" stone rings, stone stripes, etc., have been reported from treeless zones in various mountain areas and are distinguished from modern forms by weathering of the stones in

[5] The term "brodelböden" has been used by some to include other structures produced by frost action, particularly stone rings, etc. It has been used also as a genetic term, implying a particular theory of origin not generally accepted.

[6] The general term "strukturboden" is commonly applied to these features; numerous other terms are listed by Sharp (1942c).

place and by the encroachment of vegetation. Antevs' study of the alpine zone on Mt. Washington (1932) is illustrative. He found both modern and ancient stone stripes and nets in the same locality. The ancient forms differ from the modern ones in being of much larger size. Antevs postulated that the large stone nets develop only over perennially frozen ground, but that the small ones do not have this requirement. This is in essential agreement with Troll's findings on the climatic distribution of modern forms (1944), and with Zeuner's general conclusions on the significance of the various types of frost-induced induced phenomena (1945, p. 12–14).

Earth mounds or palsen.—Various types of mounds have been described from arctic and alpine environments by Högbom (1914, p. 306, Lozinski (1933), Sharp (1942c), Muller (1945), and others, and a regional summary of their occurrence has been given by Troll (1944). Some types of mounds have ice cores and collapse when the ice melts; other types are composed of soil material throughout, and can thus withstand climatic amelioration. Obviously only the latter type or types are of interest as periglacial phenomena.

Lozinski has dealt at length with ancient palsen fields of periglacial origin in the Polish Carpathian foreland and has ascribed considerable importance to this type of feature as evidence of former periglacial conditions. Lozinski was not clear, however, as to how ancient and modern palsen are distinguished, or as to how palsen formed by frost action are distinguished from soil mounds formed in other ways. He suggested that the soil mounds of the Gulf Coastal area in this country include frost-built palsen of periglacial vintage—an opinion questioned by Bryan (1940), and certainly difficult of confirmation in view of the long-standing controversy as to the origin of the mounds in question. (cf. Rich, 1934.) Periglacial origin seems more plausible, however, for the much-debated Mima mounds of western Washington (Péwé, 1948).

Amorphous disturbed soil.–The effect of differential frost action in causing some rock fragments to move up while others move down has been analyzed by Taber (1943). This process may be regarded as having a churning effect on the soil. Where ventifacts, which obviously must form at the ground surface, a found scattered at random through soil to depth of 1 or more feet, and other indicat of disturbance are found, frost action has be invoked (Bryan, 1932; Denny, 1936; Bry and Ray, 1940, p. 26; Bastin and Caill 1941). Lutz and Griswold (1939) have poi out that tree roots may simulate certain of th effects of frost in soil, and that this possibil must be eliminated before frost action is post lated.

Landslides.—Landslide masses interpreted a having moved under periglacial conditions wer described by me from an upland area in nort central New Mexico (Smith, 1936). Much o the sliding took place on slopes as low as 4°-5 and the slides are now completely stabilized The topographic relations indicate two episode of sliding well separated in time, and these ar correlated with glacial stages.

Stabilized taluses.—A talus may be said t become stabilized when the addition of new material from above has virtually ceased. Thi may come about: (1) by gradual headward en croachment of the talus upon the source area so as to cover it; or (2) by arrest of the proces of dislodging block material, before the above condition is reached. The second situation may be inferred where trees or other types of vege tation have become established on portions o the talus without interference from falling blocks, although the talus is still overtopped by steep rock ledges which constitute a potential source of new material. Since frost weathering is known to be particularly effective in provid ing material for taluses (Högbom, 1914; Blackwelder, 1935), a diminution of frost action through climatic amelioration provides a log cal explanation for the stabilization of talus at many places. On the basis of these and other considerations of a more local nature I have inferred a periglacial origin for the talus borde ing Devils Lake in the Baraboo area of Wis consin (Smith, 1941).

Nivation hollows.—The process of nivation a its effects in producing minor topographic ho lows was first described by Matthes in 19 from the Bighorn Mountains, and since the has been reported from other western moun tains by Russell (1933), from Greenland by Ekblaw (1918), and from Iceland by Le (1939). Certain "arm-chair" forms in Engla

FIGURE 1. PERIGLACIAL BLOCK STREAM
Along South Mountain, northern Maryland.

FIGURE 2. ANCIENT STONE RINGS IN RUDE NETWORK PATTERN
On Beartooth upland of northern Wyoming.

ANCIENT BLOCK STREAM AND STONE RINGS

have been attributed (Bull, 1940) to similar origin under a colder climate of the past.

Protalus ramparts.—These features are ridges of blocks that accumulate by sliding or rolling down over semipermanent snowbanks (Bryan, 1934; Bryan and Ray, 1940, p. 35). They occur most commonly in cirques. Where snowbanks of the required size and persistence no longer occur in association with these features, a former episode of cooler climate is inferred.

Minor superficial folds.—Krüger (1933) postulated that minor, irregular, superficial folds (Fig. 5) more or less split along the axial plane, and occuring in thin- to medium- bedded sedimentary rock, were produced by frost wedging under periglacial conditions. The folds die out downward within a few feet. A similar type of structure was described by Campbell (1906) from Arkansas, and attributed to the expansive effects of weathering along joints, with frost action as a contributing factor. It is unknown whether frost action is of equal importance in all occurrences of this type of structure.

Dry valleys.—The anomalous occurrence of dry valleys in rock now having subsurface drainage was noted by Reid, in England, in 1887, and was attributed by him to erosion by running water during glacial times when the substrata were made impervious by freezing. This explanation was accepted by Geikie (1894, 395-396) and reaffirmed by Bull (1940). Dry valleys believed to have been of similar origin were described from Germany by Kessler (1925).

Asymmetric valleys.—The common asymmetry of east-west valleys in areas of perennially frozen ground in Siberia was noted by Schostakowitsch (1927). In the Erzgebirge basin of Germany, Lösche (1930) found a similar degree of asymmetry, best developed, however, along northwest-southeast valleys. The steeper side is characteristically on the northeast. In some places, modern symmetrical valleys are cut down into older asymmetrical valleys, indicating changed conditions of erosion. The asymmetry was attributed to one-sided stream erosion at a time when the ground was perennially frozen, and solar exposure of the northeast side made for maximum thawing and minimum resistance to stream erosion on that side, in contrast to the greater resistance of the still-frozen ground on the opposite side. Other factors in asymmetric valley development were discussed further by Büdel (1944), Troll (1947) and Poser (1947a). Poser concluded that the asymmetry of valleys, if correctly interpreted, can provide valuable evidence of the former extent of perennially frozen ground.

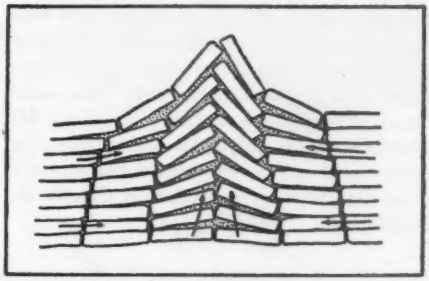

FIGURE 5.—DIAGRAM OF MINOR SUPERFICIAL FOLD, OF THE ORDER OF ONE METER IN HEIGHT, ATTRIBUTED TO PERIGLACIAL FROST ACTION

After Kruger (1933, p. 222).

Résumé.—Thirteen types of features interpreted as indicative of former periglacial conditions have been discussed here. Of these, the ones most generally applicable in areas associated with continental ice sheets are: casts of ground-ice wedges, involutions, and solifluction deposits, including block accumulations. Only the block accumulations have distinctive surface expression. All are best studied in cross section. Where they occur at the surface, they record only the last major climatic change. Where they are interbedded with other types of deposits, they serve as climatic horizon markers, may record more than one climatic change, and thus may play a significant part in the interpretation of Pleistocene stratigraphy.

"Fossil" ground-ice wedges constitute the most convincing evidence of the former presence of perennially frozen ground, and many workers consider well-developed involutions to have the same criterion value. The significance of solifluction deposits is less firmly established, but where these contain a high proportion of coarse rubble, and occur on gentle slopes, they at least strongly suggest the former prevalence of perennially frozen ground.

In mountainous areas, the ancient frost-induced features most commonly encountered are stone nets, stone stripes, and the several varie-

ties of block accumulations. Earth mounds or hummocks and boulder-banked terraces (Eakin, 1916; Antevs, 1932) are common also, but their antiquity is more difficult to prove. Stone rings, stone stripes, and related features develop only in treeless zones, and may occur with or without perennially frozen ground. According to Zeuner (1945, p. 13), heavy snowfall and protracted freeze-thaw conditions are the main requirements. Where these features are of large scale, however, association with perennially frozen ground seems probable. Troll's (1944) summary on the geographic and climatic distribution of active frost phenomena provides basic data for more particularized climatic interpretations.

Regional Studies

General.—The world-wide distribution of modern frost phenomena was summarized by Troll in 1944; this was supplemented, in 1947, by a generalized map showing the lower limit of altitude at which soil structures due to frost action occur throughout the eastern hemisphere. No comparable summary of periglacial phenomena has been made. Perhaps the closest approach was in Kessler's monograph (1925), which, however, was concerned mainly with German areas. Since 1925 a large volume of new data has become available for all parts of Europe which came under the influence of periglacial conditions during the Pleistocene. Some of this information has been referred to on preceeding pages. Much of it, although not specifically summarized, has been drawn upon by Poser in his synthesis of periglacial climatic conditions, noted in a later paragraph of this paper.

In North America, studies on periglacial phenomena are still in their infancy. The few widely scattered areas that have been studied may be listed briefly. In New England and adjoining areas in New York, stone rings and stripes have been described by Antevs (1932), frost-churned ground by Bryan (1932) and Denny (1936), and involutions and solifluction phenomena by Denny (1936; 1938). In the Pennsylvania Appalachians and the Blue Ridge area, block fields and block streams have been noted by Smith (1945) and Peltier (1945). In the South Carolina Piedmont, mass-movement phenomena described by Eargle (1940) were interpreted by Bryan (1940) as of periglacial origin. In the upper Mississippi Valley area, examples of involution layers have been described by Sharp (1942a), and of solifluction and related phenomena by Smith (1941). In the Rocky Mountain region, the only reference to periglacial phenomena was a casual one by Bryan and Ray (1940). In the Pacific Northwest, periglacial stone nets were noted by Eakin (1942), and the probable periglacial origin of earth mounds was recorded by Péwé (1948).

Reconstruction of periglacial climatic conditions.—The interpretation of periglacial climatic conditions is based to a considerable extent on frost phenomena, but draws also upon eolian phenomena, paleobiologic data, and meteorologic deduction. All these factors entered into the following major contributions on this subject.

In 1925, Kessler presented a generalized reconstruction of periglacial climatic conditions in Germany. He concluded that the climate in the entire belt between the Alpine and Scandinavian ice sheets was much the same, with a mean annual temperature not higher than -2°C., wide fluctuations in temperature, comparatively low precipitation, and dominant cold, dry winds blowing down from the northern ice, giving way at times to precipitation-bearing winds from the west and southwest.

Zeuner (1937) gave a more particularized interpretation for a larger area, during a glacial stage corresponding to the Würm maximum. He recognized greater regional differences in climate than did Kessler and showed the following climatic zones, from north to south, on a generalized map: (1) a comparatively narrow tundra belt extending from southern England across northern Germany and Poland; (2) a broad loess belt, or grass steppe, covering much of northern France, Germany, Poland, and parts of bordering countries; and (3) a southerly forest belt. Climatic conditions in each belt were analyzed, and differences from east to west were noted. The widespread occurrence of perennially frozen ground was affirmed. The dust deposited in the loess zone was believed to have been derived largely from the comparatively barren tundra zone.

Cailleux, in 1942 (*see also* Wright, 1946), interpreted periglacial wind action from the distribution of ventifacts and eolian sand grain

in Pleistocene deposits. His composite map for the entire Pleistocene (Fig. 16, p. 70) shows highest percentages of eolian sand grains and thus indicates most vigorous wind action, in a zone corresponding roughly to Zeuner's tundra belt; his findings agree essentially with Zeuner's interpretation.

Probably the most comprehensive reconstruction of periglacial climatic conditions yet published was that of Poser (1947a; 1947b) for the Würm glacial stage in Europe. Generalized maps showing the following climatic data were presented; (1) southern limit of the belt of perennially frozen ground; (2) depth of summer thaw; (3) intensity of frost action in winter; (4) wind systems in summer and in winter; and, (5) climatic subdivisions (Fig. 6) of the region, comprising the following: (a) tundra climates (maritime, continental, and intermediate) with perennially frozen ground; (b) continental forest climate with perennially frozen ground; (c) maritime tundra climate without perennially frozen ground; and (d) maritime forest climate without perennially frozen ground. Poser's tundra belt includes a large part of Zeuner's loess belt, and his boundary for the forest belts differs considerably from Zeuner's.

In North America, data now available are far from adequate for the types of interpretation outlined above. The work of Bryan and Cady (1934), however, represents a climatic interpretation of a more limited nature, based partly on eolian deposits but largely on meteorologic deductions.

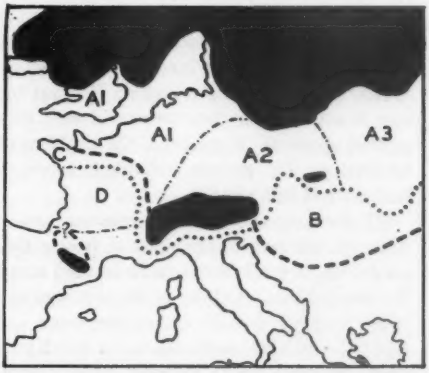

FIGURE 6.—CLIMATIC ZONES IN EUROPE DURING THE WÜRM GLACIATION, ACCORDING TO POSER (1947b, p. 266)

Heavy dashed line represents the southern boundary of the area of perennially frozen ground; heavy dotted line marks limit of the arctic forest. Light dot-and-dash lines indicate boundaries of climatic zones where not shown by above lines. *A* represents tundra climate with perennially frozen ground (*A1* is a glacial-maritime province; *A2* intermediate province; and *A3* glacial-continental province); *B* represents continental forest climate with perennially frozen ground; *C* represents maritime tundra climate without perennially frozen ground; and *D* represents maritime forest climate without perennially frozen ground. Glacial ice shown in solid black.

Problems

(1) *Problems of terminology.*–The terminology of frost action and periglacial phenomena is in a state of considerable disorder. Many terms are used with different meanings by different workers. The term *solifluction*, for example, has been used to mean mass movement both with and without perennially frozen subsoil; although most writers use it to mean progressive downslope movement, some include nonprogressive differential movement of the type involved in the formation of stone nets. The term *periglacial* itself is not beyond criticism. It is perhaps unfortunate that this term has geographic connotations; in a strict sense, it denotes simply the environmental conditions marginal to an ice sheet, but by established usage it applies specifically to that zone in which the cooling effect of the ice sheet itself produced a frost climate (Zeuner, 1945, p. 55)–a zone "characterized by low temperatures, strong winds, and many fluctuations across the freezing-point at certain seasons." (Sharp, 1942a). The term is a general one, and useful as such; supplementary terms of more limited and explicit meaning, however, might be helpful. When the term *periglacial* is extended to refer to conditions of lowered temperature, during glacial stages, at places remote from glaciers, as in mountains and upland areas, criticism is perhaps justified; a new term to denote climatic rather than geographic approach to glacial conditions might be preferable.

In many instances, different terms are used by different writers in referring to the same phenomena. Sharp (1942c), for example, lists 26 terms used for stone rings and stone nets; it is probable that there are many varietal differences that warrant distinction, but very doubt-

ful whether any such distinctions are implied by the terms listed.

Terms of definite meaning promote clear thinking, and standardization of such terms promotes the interchange of information among workers. The desideratum is a precise terminology that is internationally acceptable, as in paleontology. Bryan (1946; 1948) endeavored to meet this need by proposing a new set of terms for the major concepts involved in the study of frost action and frozen ground. It is yet too soon to say whether these terms will meet with general approval; if accepted, the problem of terminology for various individual types of features will still remain.

(2) *Problems of origin and criterion value.*—Although the general principles of frost action are known, much remains to be learned about the detailed characteristics of the processes and of the resulting deposits and surface forms and about the limiting conditions under which particular features are developed. Closer parallels for phenomena interpreted as periglacial need to be sought and studied in regions where they are now being formed. How, for example, and under exactly what conditions, does the so-called process of solifluction move large volumes of coarse rubble long distances on low gradients? Just how are involutions formed? To what extent is the size of stone rings a function of climate, and what part is played by other factors, such as lithology and stage in the developmental process? Answers to these and related questions will involve continuous observation or periodic re-examination of selected localities, excavation to study subsurface characteristics of many features and other methods of study. Laboratory experiments also may play a part.

(3) *Problems of distribution.*—Much work remains to be done before our knowledge of periglacial frost phenomena in North America can compare with that for Europe. The areal distribution of particular features needs to be outlined, and stratigraphic distribution of buried features must be studied. In mountains, the distribution of various forms with respect to altitude and latitude needs to be ascertained. In this work, representatives of several different fields may have a part. As knowledge of the subject becomes more widely disseminated, considerable information on distribution of the more conspicuous features should be provided as a by-product of field studies in other branches of geology. Ancient periglacial features, however, are not always easy to find or to identify. In many places they are obscured by vegetation, soil, or colluvial deposits and in other places they probably grade into soil materials being moved by present-day creep. Under these conditions, the features in question are likely to be unrecognized unless specifically sought for. Collaboration between geomorphologists and soil scientists should be fruitful. It is the soil scientist whose studies of surficial materials are most intimate and who is best qualified to evaluate discontinuities in the soil profile, or other anomalous relationships. Archaeologists and paleontologists also may contribute through their detailed examination of particular places.

(4) *Reconstruction of former climatic conditions.*—A major objective in the study of frost phenomena is the interpretation of past climatic conditions on a regional scale. This requires that adequate information on the regional distribution of particular features be assembled, integrated with the evidence provided by other physical phenomena and by fossil floras and faunas, and harmonized with established climatologic knowledge.

(5) *Testing value of buried frost-induced features in the interpretation of Pleistocene stratigraphy.*—In Europe, the recognition of the interbedding of solifluction deposits and other frost phenomena with loess, and alluvial terrace deposits in the periglacial zone has been helpful in deciphering the Pleistocene stratigraphic record. It remains to be ascertained whether a similar method of approach will prove fruitful in this country.

Stream Terraces

General Statement

For the purpose of this discussion, stream terraces, may be defined as remnants of former valley floors standing higher than the stream gradients in the present cycle or epicycle of erosion. Two main types may be distinguished:

(1) Terraces cut on bedrock by lateral planation, and veneered with the fluvial deposits associated with that process. Such terraces generally match in height on opposite sides of the valley, unless the surface is raised locally by

slopewash from bordering areas (Mackin, 1937). This type of terrace is generally attributed to tectonic movement and is important in the study of such movement. Under special circumstances, lowering of stream grade by piracy is a possible cause also. Mackin (1937) postulated climatic change as still another possible cause, suggesting that downcutting may have resulted from climatic changes related to glacial stages. He failed to explain, however, why there was not a reversal to aggradation during interglacial stages.

(2) Terraces developed in alluvium previously deposited by the same stream which cuts down into it (alluvial or cut-and-fill terraces). In other words, the normal course of degradation is interrupted by aggradation. The secondary episode of degradation may take place in either of two ways: (a) By continuous lateral swinging of the stream during downcutting, as described by Davis (1902). This results in intermediate terraces which are irregular in ground plan and generally do not match in number or in height on opposite sides of the valley. Such terraces are of little historical significance. (b) By comparatively rapid downcutting followed by more leisurely valley widening and/or reaggradation. The amount of downcutting may equal, exceed, or fall short of the depth of the original bedrock floor. Intermediate terraces between the top of the initial fill and the bottom of the final valley may result either from pauses during downcutting or from further alternations between degradation and aggradation, as described by Lueninghoener (1947) from eastern Nebraska. Terraces formed in either of these ways match in height across the valley.

Terraces of type (2b) are of particular interest in studying the effects of Pleistocene climatic changes, and form the subject matter of the following discussion. Only a brief treatment is given here, pending a more detailed analysis in a future publication.

Alluvial terraces of type (2b) may result from: (1) eustatic changes in sea level; (2) effects of glaciation on load and volume of streams heading in glaciated areas; (C) effects of climatic change on regimen of streams heading in nonglaciated areas; (4) crustal warping; and (5) combinations of the foregoing. Some of the basic principles underlying the interpretation of these terraces have been outlined by Mackin (1948), and a quantitative method of study has been suggested by Jovanović (1940), and reviewed by Lewis (1947).

The relation of eustatic changes in sea level to stream terracing has been discussed by Daly (1934) and Zeuner (1945), and theoretical considerations have been set forth by Mackin (1948). Terraces ascribed to the combined effects of crustal warping and eustatic changes have been described from Louisiana by Fisk (1939; 1944).

Where terraced valleys head in glaciated regions, the relations of the terraces to glacial stages may be investigated by continuous tracing into morainal areas. In many places, it is found that aggradation was effected by deposition of glacial outwash, and that degradation took place during nonglacial intervals. A classic example was described from the Alps by Penck and Brückner in 1909 (reviewed by Wright, 1937). Differentiation of the terraces in that region, in fact, played a significant part in establishing the glacial sequence. Development of the successive terraces was conditioned both by changes in base level and by the effects of glaciation on stream action. Terrace sequences such as this serve to carry the glacial chronology into unglaciated territory, but in most places the record is less complete than in the Alps, particularly with respect to the earlier glacial stages. Examples in other regions are provided by the studies of De Terra and Paterson (1939) in India, by MacClintock (1922) and Thwaites (1928) in the upper Mississippi Valley area of this country, and by Bryan and Ray (1940) in northern Colorado.

Where both eustatic changes in sea level and direct glacial influence can be ruled out, only climatic change and crustal warping are left to account for terracing. And where the terraces are comparatively uniform and widespread in different drainage areas, the crustal movements required to account for terracing would be, as Huntington (1905; 1914) pointed out, of such delicate adjustment and complex pattern as to be altogether incredible. Climatic change alone thus remains as the logical explanation of terracing in many regions. If the true nature and sequence of the climatic changes involved in the development of a given set of terraces can be interpreted satisfactorily, and can be

correlated with glacial climatic changes, a connecting link between chronologies in glaciated and nonglaciated regions is provided. The problems entailed in this mode of approach are outlined.

Problems of Climatic Terraces

Although it is generally agreed that terracing is produced by climatic changes, the question as to particular types of climatic shift responsible for aggradation and degradation, respectively, has been controversial. Huntington (1914), who originally expounded the concept of climatic terraces, stated that increasing aridity led to aggradation and decreasing aridity to degradation. This view was shared by Blackwelder (1931) and by Wenzel *et al.* (1946). The opposite interpretation, however, was made by Albritton and Bryan (1939), Pfannenstiel (1940), Bryan (1941), Hack (1942), and Schultz and Stout (1945), all of whom correlated aggradation with more humid conditions and degradation with more arid conditions. This, actually is less contradictory than it might seem. For the most part, the workers of opposed viewpoint were considering different drainage areas where different conditions prevailed. Barrell (1908) long ago pointed out that the effects of a given climatic change would be different even in different stretches of the same stream. Cotton (1945) and Richardson (1945) more recently have pointed out some of the other complicating factors involved in the climatic interpretation of terraces. It may be concluded that no simple generalization will apply to all terraces, and that each terrace system must be analyzed in the light of its own particular setting. Due consideration must be given to local climatic environment and topographic conditions, to changes in conditions along the stream course, changes in amount and character of detritus fed to the stream by weathering and mass movement, effects of climatic change on vegetation and thus on ground protection and on rate of runoff, and changes in maximum, minimum, and mean discharge entailed by the climatic shift. Where possible, deductions from these factors need to be supplemented by the evidence of the terrace deposits themselves, including composition, stratification, degree of sorting, texture (*cf.* Zeuner, 1933), cementation, surface soils and buried soils, and age and ecol implications of any fossil animals or pla contained in the terrace deposits. (*cf.* Albrit and Bryan, 1939.)

A special case of climatic terracing is that streams heading in former periglacial zon Owing to accelerated supply of material streams by frost weathering, mass moveme and associated processes, aggradation took pla during glacial ages and degradation under no glacial conditions. Examples from areas bo dering the Alps are given by Büdel (1944). Th possibility of climatic influence on the acc mulation of pre-Wisconsin, nonglacial terra deposits in the Driftless area of Wisconsin wa discussed by Thwaites (1928), and periglacia origin of these deposits would seem a logic working hypothesis. The same hypothesis seem applicable to younger alluvial terraces describe from the same area by Bates (1939), althoug this possibility is overlooked by Bates.

Regional Studies and Problems

In Europe, detailed terrace studies have bee carried on in many of the major drainag basins, and correlations with glacial event have been made. The general results have bee summarized by Woldstedt (1929), Wright (1937), and Zeuner (1945).

Some of the terrace studies in Asia and Africa as well as in Europe, have been reviewed, and correlations have been postulated, by Paterson (1941), in connection with a theory of climatic influence rigorously criticized by Cotton (1945).

In North America, the areas in which allu vial terraces related to the chronology of Pleistocene climatic changes have been described in any degree of detail are comparatively few and widely scattered. In the upper Mississippi Valley, the work of MacClintock (1922) and Martin (1932) deserve mention. In the lower Mississippi Valley, Fisk's work (1944) is noteworthy; correlations with the upper valley, however, are on a tenuous basis because of inadequate published information on the latter area. In eastern Nebraska, a detailed study of one area was made by Lueninghoener (1947). In the Colorado Rockies, the work of Bryan and Ray (1940) stands by itself. In western Nebraska a preliminary account of terrace phenomen

has been published by Schultz and Stout (1945), and a more detailed local study was published by Wenzel *et al.* (1946). Correlations with the work of Bryan and Ray were suggested by Condra and others (1947).

In the southwestern states, terraces have been studied at various places by Albritton and Bryan (1939), Hack (1942), and others. Regional correlations were discussed by Bryan (1941). Thornthwaite and his co-workers (1942), however, took issue with the climatic interpretation of terraces in the area studied by Hack; they differed, apparently, in their conception of what constitutes evidence of a climatic change.

It is evident from the brevity of this list of studies that large areas remain to be covered, and that continuous tracing of terraces along individual stream systems is needed. In such studies, both the morphology of the terraces and the character of the terrace deposits are important. The value of subsurface methods in studying the latter has been demonstrated (Fisk, 1944) and warrants further application wherever feasible. When placed on a regional basis, studies of alluvial terraces may come to play an important part in the correlation of events between glaciated and nonglaciated regions, particularly with respect to the later stages of the Pleistocene.

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PLEISTOCENE RESEARCH

A REVIEW BY THE MEMBERS OF THE COMMITTEE ON INTERRELATIONS OF PLEISTOCENE RESEARCH, NATIONAL RESEARCH COUNCIL

12. INTERRELATIONS OF PLEISTOCENE GEOLOGY AND SOIL SCIENCE

BY JAMES THORP

INTRODUCTION

The study of soil is the field of research in which the geologist, the biologist, the climatologist, the agriculturist, the archaeologist, and the engineer meet. Reports on Pleistocene[1] studies are of inestimable value to the soil scientist; but, in spite of the great usefulness of the work already done, there are still many ways in which it can be improved to make it more useful to the soil scientist. For example, Qal (Quaternary alluvium), on the map, tells the soil scientist nothing of importance that he cannot see as he drives down the road. A good map of Pleistocene alluvium, showing stratigraphic relationships, texture, and lithologic character of the deposits, in broad terms, will enable the soil scientist to understand better the genesis and morphology of the soils, to draw better soil maps, and to improve his system of soil classification.

Detailed soil surveys and laboratory investigations of the soils developed in Pleistocene deposits can be of great aid to the Pleistocene stratigrapher who has learned to interpret soil maps; but soil-survey maps and reports can be improved also, in many ways, to make them more useful to the geologist. It might be well, for example, for the soil scientist to adopt a system of soil-horizon nomenclature that will include the entire regolith and to devote more attention to deep layers of earth material. Recent observations show clearly that the regolith may be modified by soil-forming processes to depths of many feet below the "B horizon" of the soil proper. Information on this material is of great use to engineers who are much less concerned about technicalities of soil-horizon nomenclature than they are about physical properties of mantle rock. Soil-survey reports would be more meaningful to geologists if they gave more information on the known stratigraphic sequence and lithologic character of parent rocks, even if exact geologic correlations are not possible.

Since soil is one of the most important basic resources of mankind, and since a large share of the most productive soil of the world is developed in deposits of Pleistocene age, there is great need for expanding Pleistocene research and for improving the techniques of investigation.

Types of information needed from geologists to make Pleistocene research of most use to the soil scientist are discussed and ways are suggested by which the soil scientist can be of greater assistance to the geologist than he has been in the past. Some of the significant literature is recorded, but time has not permitted the digestion of an extensive bibliography.

TYPE OF INFORMATION NEEDED BY SOIL SCIENTISTS

I. *Character of Pleistocene Deposits.*—In many reports on Pleistocene geology, greatest emphasis is laid on the stratigraphic succession of deposits with relatively less emphasis on the texture, clay types, lithologic character, soluble salt content, degree of weathering, and degree of stoniness of deposits.

1. Texture: Glacial drift and other Pleistocene deposits might be classed as very sandy

[1] "Pleistocene," as used here, covers the entire time between the end of the Pliocene and the present.

moderately sandy, medium-textured (including silty), and clayey. Perhaps still a fifth texture group, clay, would be useful in many instances. Generally, it is important also to know whether the deposits are stratified or unstratified. The texture of Pleistocene deposits, combined with other physical and chemical characteristics, limits the range of possible soils that can develop.

2. Clay types: Not only is the proportion of clay important, but the general type of clay is of equal significance to the kind of soil that will form. A general grouping of clays, like "kaolinitic," "montmorillonitic," "allitic," etc., would be adequate as a basis for soil investigations.

3. Lithology: Most Pleistocene deposits have several lithologic facies that are highly significant for soil development. Sub-division of Pleistocene deposits on this basis is as important to the soil scientist as separation of deposits of different ages. Not only do we need to know the kinds and proportions of the rock types present, but it is sometimes of economic interest to know what rare elements (*e.g.*, cobalt or boron) may be lacking. Studies of this kind would require close co-operation of soil scientists and geologists. Where Pleistocene maps and reports fail to show these differences, it is necessary for soil scientists, many of whom are less skilled than geologists in the identification of rocks, to work out these details themselves.

4. Salts: The presence of easily soluble salts, like the chlorides, sulphates, bicarbonates, and carbonates of various metals, and of the less-soluble salts like calcium carbonate, gypsum, etc., have controlling effects on soil structure and vegetative cover. It is especially useful to know what correlations exist between salt content and Pleistocene deposits of given age. Most recent studies of Pleistocene deposits give information of this sort.

5. Leaching and weathering: It is useful to know the degree and kind of leaching and rock weathering in each deposit. Geological studies usually bring out this information in some degree; but some of the work on the Pleistocene is inadequate in this respect. The degree of leaching and weathering of Pleistocene deposits far from the limits of glaciation, as in the coastal-plain and river-terrace deposits of southern and southeastern States, gives clues to the character of the parent material and of the length of time required for the formation of soils of given types. To what extent, for example, were the now-acid Pleistocene deposits formerly calcareous, and how deep has leaching proceeded?

6. Stoniness: The degree of stoniness of soil material affects the tillability of the soil, and it is also important to engineers who expect to use the soil for construction purposes. Most Pleistocene geologic reports give attention to the degree of stoniness of the deposits.

II. *Recent Trends in Study of Physical Properties of Pleistocene Deposits.*—Bushnell's "The Story of Indiana Soils" (1944) gives an excellent summary of the properties of Pleistocene deposits in Indiana that are significant to soil formation; and his key to Indiana soils shows the interrelations of these materials with natural drainage, topography, vegetation, and other features of the natural landscape. A similar trend of emphasis is noticeable in the study of soils throughout the United States as witnessed by many publications. The basic information and most of the actual boundaries for recognizing and mapping the eolian deposits of Indiana are in Bushnell' publication. Unfortunately, however, the material will not be fully usable for this purpose until a competent Pleistocene stratigrapher has gone over the ground with a soil scientist. Some of Bushnell's aerial photographs show a gross pattern of dark soils in a polygonal network of depressions, with light-colored soils on micro-knolls between, that suggest relict effects of frost action. I believe that a careful study of the work of Troll (1944), Bryan (1946), and H. T. U. Smith (1928) may throw new light on the genesis of some of the "black and clay" soils of the north-central States. In many places frost action during late Pleistocene times may have contributed to the micro-relief so important to the formation of a pattern of light and dark soils.

A very useful booklet on permanently frozen ground and its effects on soils was compiled by the U. S. Geological Survey (1943) during World War II. The compilation covers studies made on the "active layer" of periodically thawed soils in the Arctic and Subarctic regions of Eurasia and North America.

Zeuner (1945) also summarizes the effects of

freezing and thawing above a permanently frozen substratum and describes periglacial phenomena, like stone rings and soil polygons, that are still recognizable in present-day soils. Zeuner also recognizes the importance of the mineralogic composition of soil materials to the kinds of soils that are developed—*e.g.*, parent materials of Podzol soils are dominated by quartz.

Guy D. Smith (1942) has published a very important recent study of the relations of soils to the thickness and texture of loess in Illinois. He found that soils with tight "claypan" subsoils are characteristic of thin loess, while less clayey and more friable soils are developed from thick deposits of the same loess sheet. His studies apparently demonstrate that weathering and soil formation kept pace with loess deposition where the loess is thin, but that soil development was retarded where loess is thick, because accumulation of eolian silt was more rapid than weathering. Hence, loess of the same geologic age is the parent material of soils of quite different stages of formation or degrees of development.

Painstaking field studies of physical properties of the so-called "Grundy soils" of Nebraska, made by Hayes in 1927 can now be interpreted to draw the same conclusions as those reached by Smith in Illinois. This interpretation of Hayes' work is now leading to a much better understanding of the genesis of the extensive "claypan" soils of Nebraska, Kansas, and Oklahoma. Furthermore, because of these soil-loess studies, we are now learning to recognize eolian deposits far beyond the geographic limits shown on maps of loess deposits of the United States.

III. *Physiographic and Topographic Relationships.*—The soil surveyor is guided in a general way by the topographic pattern when he draws boundaries between soil types. Where the Pleistocene deposits are complicated, topography may be inadequate as a guide for drawing soil boundaries, and an understanding of the stratigraphic sequence and of unconformities will go a long way toward making it possible for the soil surveyor to draw a good map in a reasonable time.

Because of their relationships to the time factor and moisture effectiveness, physiography and topography are almost as important to soil formation as is the character of the deposits. Modern soil surveys generally show much detail of slope gradients. Some attention also has been given to the texture or fabric of topography; that is to say, the length and pattern of slopes and the distribution of highs and lows which are significant to run-off, run-on, and water absorption in soils. Most Pleistocene geological surveys also give information regarding the degree of slope and texture of the landscape. Soil scientists and geologists need to consult on this problem to determine the most practical classification for general use. The degree and character of slope have much to do with the rates at which water runs off or disappears into the soil. Many glaciated landscapes have myriads of depressions from which there is no natural surface drainage. The character of soil on a given kind of material depends largely on whether there is any means for water to be drained out through subterranean aquifers. The moisture regime is one of the most important factors in soil development and in the suitability of soils for use. This kind of information is easily obtained by the soil scientist, and is also provided by glacial geologists.

Cumberland (1944; 1947) demonstrates that geologic and geomorphic land characteristics in New Zealand had already loaded the gun for a cycle of catastrophic soil erosion ready for the white man to pull the trigger when he first brought his culture to the islands. Good land use is recommended instead of "fighting against nature," to prevent complete ruin of the land in many parts of the country. This work is in line with the great stress currently placed in the United States on the effects of slope and soil character on the problems of soil erosion and conservation. Publications on soil erosion are almost beyond counting; but an excellent summary of the soil conservation problem has been prepared by Mark Baldwin of the Food and Agricultural Organization of the United Nations (1948).

It is of value to have some estimate of the geologic age or physiographic status of the present land surface. For example, is the present topography essentially as it was in Wisconsin or Illinoian times, or has post-Illinoian or post-Wisconsin dissection destroyed the old soil and

started a new cycle of soil formation? In eastern Nebraska, where several soils have developed primarily in Kansan till, only very small areas of the soils show evidence that they have been developing ever since the first exposure of Kansan till to soil-forming processes. Detailed physiographic studies will probably show that some soils on Kansan till began to develop at the end of the Iowan subage, whereas others began to develop at various times thereafter, the latest probably very recently. The evidence is in the depth of leaching and weathering and in the degree of development of soil profiles; but physiographic studies are needed to determine exact correlations and so to get some idea of the length of time required for profiles of given kinds to be formed. Evidence is already at hand that relationships exist between soil age and soil fertility. A knowledge of whether the present topography is constructional or destructional gives a clue to soil age and rate of soil formation.

The soil surveyor's job is lightened considerably if he has advance information on the direction and extent of ice movement in glaciated areas, and the dominant sources of sediments in alluvial and loessial deposits outside the regions formerly covered by glaciers.

IV. Stratigraphic and Genetic Relationships of Pleistocene Deposits.—1. Stratigraphy: Many stratigraphic relationships of Pleistocene deposits can be shown in cross section but cannot be shown on maps of the scale adopted for survey. Admirable treatment of this problem may be seen in the Pleistocene sections in the works of Kay (Kay and Pearce, 1920), Condra, Reed, and Gordon (1947), and a number of others in the United States. A great amount of similar work, much of it antedating that in the United States, has been done in several European and Asiatic countries. Zeuner (1935) and Flint (1947) give good summaries. Scales large enough to show the distribution of each Pleistocene deposit should be adopted where feasible. Otherwise, geologists might publish supplemental large-scale sample maps of small areas, selected to show the geographic and topographic relationships of each of the separate Pleistocene deposits. This sort of sample map would be especially useful in areas like eastern Nebraska and southwestern Iowa, where many Pleistocene deposits are superimposed, with only very narrow outcrops. Soil scientists with the aid of geologists have already made considerable progress on this type of investigation, but most of the work is unpublished.

2. Buried soils: The presence in Pleistocene deposits of buried soils, of leached and weathered zones, and of buried loess is of great significance to soil formation, especially in deeply dissected country where such deposits crop out along the slopes. The degree of weathering and leaching is related directly to fertility problems in many areas. Many soil surveyors are not qualified to unravel the stratigraphic sequences of deposits in these places, and a good Pleistocene map with diagrams and explanations helps the soil surveyor to understand what he finds in hilly country, and so to arrive at decisions as to how best to classify the soils. Drilling programs, like those of the Conservation and Survey Division of Nebraska, and other State and Federal agencies interested in ground-water studies, provide much incidental information of this kind.

Although buried soils of many kinds and degrees of development have been observed and recorded in print in many different countries, we find few references in which the profiles of the soils are described in sufficient detail to assure identification of the great soil groups to which the soils belong. One cannot always be sure, for example, whether a dark buried soil is truly a Chernozem or whether it is a Wiesenboden, or perhaps a buried Half-Bog soil that was developed in a wooded swamp. Zeuner (1945) seems to have avoided the easy error of mistaking buried Wiesenboden for Chernozem, and he rightly warns against mistaking dark manganiferous layers for buried soils. However, he is mistaken in his statement that Chestnut soils are calcareous throughout, since many of them are leached of carbonates to variable depths. His interpretation of dynamics in Chernozems seems faulty in that he assumes upward capillary action to be responsible for the accumulation of carbonate of lime in the subsoil. Significant upward capillary movement would require a water table within 5 or 6 feet of the surface. This condition does not exist in most Chernozems.

When one reads Erhart's paper on a Pleisto-

cene "paleosol" in the Bas-Languedoc (1940) one wonders whether the dark color of the soil developed in loose volcanic material is due to a former grassy vegetation as proposed by the author, or whether the volcanic materials may have caused organic material to accumulate from the partial decay of forest debris. Certain volcanic ashes cause the formation of black humic soils, even under forest cover and with good natural drainage, with somewhat darker color and more humus than will develop in the Chernozem "steppe." Generalizations about soils in relation to vegetation must be made only with consideration for all known facts.

Kay's publications on the gumbotil of Iowa, summarized first in 1916 and later in 1920 and 1930 (*17*), indicate clearly that gumbotil is the product of soil-forming processes, even though Kay does not say in so many words that gumbotil is "fossil" soil or buried soil. He also makes it clear that some of the "gumbo" is developed in loess or other material that overlies the till.

Most writers on the Pleistocene of North America mention buried or "fossil" soils. For example, Lugn (1935), Condra, Reed, and Gordon (1947), Schultz and Stout (1945), Flint 1947, pages 483–85), Thwaites (1941), Bryan (1948), and many others here and abroad use buried soils as stratigraphic markers. Of the literature so far reviewed, however, only Bryan's paper gives detailed descriptions of the buried soils adequate for sure identification of the great soil groups or for interpretation of the climatic conditions under which the soils probably developed. The next step in this field is for pedologists to examine a large number of the buried soils, describe their morphology in detail, and collect samples for laboratory analysis. This will give a far better foundation for interpretative studies than now exists.

The writer has seen many places in the United States where soils apparently are relict rather than "fossil." Physiographic evidence suggests that they began to develop during early or middle Pleistocene time and have been neither eroded nor buried. Their present characteristics have to be ascribed to all the conditions that have existed since they began to develop rather than only to those that now prevail. The fossil soils are those that have been preserved by burial. The organic matter is modified and partly destroyed after burial, and some of the soils are modified further by oxidation, reduction, solution, and precipitation. Major identifying characteristics usually are preserved. This is a fertile field for research.

Relict effects of past climatic and geologic history, involving the Pleistocene, in part, are discussed by Crocker in a series of papers on soils, ecology, and geology of parts of Austrialia. He demonstrates (1946) the importance of these studies to an understanding of widespread minor-element deficiencies in soils, especially those of copper and cobalt.

> "The most important paleo-pedological influences have been, (1) the building up of extensive calcareous dune systems and sand sheets during the Pleistocene glaciations, (2) the continuous solonizing influence of cyclic salt, and (3) a severe post-glacial arid period." (p. 5)

He mentions the importance of loess, blown from calcareous sand, as a source for lime-carbonate concretions in "mallee" soils.

Another Australian pedologist, C. G. Stephens, has contributed a number of papers at least one of which bears on the effects of relict soils on the genesis of soils in "recent" times. Among these, his *Pedogenesis following the dissection of lateritic regions in Southern Australia* shows how Pleistocene erosion has dissected the old laterite-soil plains and exposed, on the slopes, the various layers or horizons of the ancient laterite soil with its subsoil of kaolinite. The character of the colluvial and alluvial soils below the slopes, as well as the residual soil on the slopes, is affected by the mineral poverty of the laterite soil. New soils from old ones, in this instance, are poor indeed!

3. Climatic and ecologic fluctuations: Some soils, now at the surface, have been in process of development since before the Wisconsin Glacial age, and others date back even as far as Pliocene times. These older soils have passed through several fluctuations of climate and several ecologic successions which certainly must have altered the rate and direction of development. A better understanding of climatic-ecologic fluctuations and of the old soils related to them doubtless could be reached by co-operative studies and would contribute to the solution of practical problems in land use. The extensive

literature on past climatic changes has not been sampled sufficiently to be reviewed by the present writer. One very short but interesting paper in this field (Veatch, 1938) suggests that the strongly developed *orterde* and *orstein* horizons of Podzol soils in Michigan are strong evidence of a former moister climate than the present one. He believes that a high degree of humidity is required for the formation of Podzol profiles with horizons of these kinds.

V. *Subjects that will Contribute to Our Knowledge of Soil Genesis and Rate of Soil Formation.*—Many loose statements have been released regarding the length of time required for a given thickness of soil to form, the most frequently quoted one being that "it takes a thousand years to make one inch of soil." Obviously this sort of statement without clarification is not only meaningless, but is actually misleading. Nearly everyone knows that several inches of soil can be formed in some materials in a matter of 5 to 50 years, while some other kinds of materials could not possibly produce an inch of soil in 10,000 years. Lines of study that would contribute greatly to our knowledge as to the rate of soil formation are as follows:

1. Soil profiles of known ages as determined by studies of tree rings, varved clays, and archaeologic sites of known antiquity should be studied and described by soil scientists in co-operation with geologists to determine the rate of soil formation and the character of soils that can be developed in a given length of time under a given set of environmental conditions. Bryan and Albritton (1943) did some pioneer work in this field that offers a promising technique. Their work covered soil development that can be dated historically.

2. The study of pollens in "fossil" soils or buried soils should be made to determine the probable climatic conditions under which these soils have formed. A comparison of these buried soils with those that can be dated in terms of years should enable soil scientists and Pleistocene geologists to make better estimates of the length of time represented by soils formed between times of glaciation. Allowance must be made for climatic fluctuations. By close co-operation with soil scientists and geologists, it is believed that the approximate rates of formation of soils of different types can be determined. With this information, it will be possible to estimate the ages of our present soils and also to fix more accurately the rates of erosion of the general land surface. Studies of this sort should make it possible to estimate the extent to which old land surfaces that have remained essentially uneroded for long periods have been mantled by glacial, eolian, or alluvial deposits at fairly recent times. Some of the very thin mantles are hard to identify, but they have rejuvenated ancient soils that would otherwise be low in fertility.

3. More emphasis is needed on Pleistocene studies outside the glacial and periglacial (loess and outwash) deposits of the United States, to determine the relative and, to whatever extent possible, the actual ages of deposits in which soils are forming. Many differences in crop yields and suitability of land for use are not reflected clearly in the visible characteristics of the soil profiles. Doubtless some of these differences are related to the age of the deposits, the younger deposits having deteriorated less than older. Problems of this sort are not confined to lower terrace levels of streams, but are also common on the uplands where eolian deposition or erosion and redeposition have been active in the Pleistocene epoch. The geologist can be of considerable help to the soil scientist in working on problems of this nature.

4. The Pleistocene loess deposits of North America, as a group, are among the most extensive soil materials of the continent. The total area of loess in the United States may equal to surpass the total area of strictly glacial deposits.

Soil scientists have contributed more in recent years to the study of loess than have geologists. There is need for more co-operative work in the field, so that the geologist can bring his techniques to the problems of sources, relative age, thickness, and composition of the loess. The soil scientist can contribute his knowledge of the relationships of soil-profile characteristics to the factors of time, vegetation, climate, and moisture regime as affected by topography. Fortunately, geologists in several States are again active in the field of eolian deposits, and co-operative work is proceeding along the lines suggested above. Both geology and soil science are fully represented in the newly formed

National Research Council Committee on the Study of Eolian Deposits of the United States and Canada.

Brown and Thorp (1942) made field and laboratory studies in 1942 of the soils of the Miami family and Miami Catena in which considerable emphasis was placed on the relationships of soil characteristics to Pleistocene deposits. Laboratory evidence was offered to show the possibility of loess as a soil material in parts of Indiana and Ohio, where it has not been generally recognized by geologists and soil scientists.

Contributions of Soil Science to Pleistocene Geology

Soil scientists have gathered a vast store of information on soils, much of it applicable to problems in Pleistocene research. More than half of the arable land of the United States and considerable nonarable land has been covered by soil surveys of varying detail. It is estimated that in more than half, and possibly in as much as two-thirds of the area surveyed, soils are developed in Pleistocene deposits. Thousands of chemical and mechanical analyses are on file, and a large share of them have be published. Soil scientists have done a great amount of pioneer laboratory work in the field of clay types and rock weathering. All of this store of information is raw material available and waiting for the use of the Pleistocene geologist. It will attain its greatest practical and scientific usefulness only when soil scientists, geologists, agronomists, foresters, biologists, geographers, and engineers pool their fields of knowledge and work out systems of classification and correlation that will meet the needs of all.

Extensive summary statements on the morphology, genesis, geography, and classification of soils, including some reference to Pleistocene geology, may be seen in the following publications:

(1) *Soils of the United States* by C. F. Marbut (1935), includes a discussion of the morphology, genesis, and geography of soils of the United States, and a map of the major soils, scale 1:2.5 million, by Marbut and Marschner. It is a summary of the soil data from hundreds of Federal-State soil survey maps and reports, and of Dr. Marbut's extensive field work in the United States carried out while he was Chief of the Soil Survey.

(2) *Soils and Men*, the 1938 Yearbook of the U. S. Department of Agriculture (1938), is devoted to the investigation, classification, and use of soils. It is the best summary of the work of agricultural soil scientists in Federal and State Government service.

(3) Kellogg's *The soils that support us* (1941) includes a clear, concise, and readable semi-technical introduction to soil science, and a treatment of the relationships of man to the soil. This is an excellent summary for the busy reader.

(4) *The principles of soil science* by 'Sigmond (1938) fulfills its title admirably. 'Sigmond offers a unique classification of soils that embodies many good points of other European and American soil scientists. His work in the field of grassland and alkali soils is especially good, partly because it is based on his own field and laboratory work in Hungary. His book includes a valuable small-scale map of the soils of Europe.

(5) Robinson's *Soils, their origin, constitution and development* (1936) and Sir John Russell's *Soil conditions and plant growth* (1937) together present a good cross section of soil science in Great Britain. Both books have wide circulation and use throughout the world. New editions of both are now in preparation. Geologists probably will find the former more useful than the latter for interpreting Pleistocene soil phenomena.

(6) Glinka's *Die Typen der Boden-bildung* (1927) translated to English by Marbut, is the classical western-language summary of Russian contributions to soil science. It emphasizes the great importance of climate, vegetation, and time as factors of soil formation. Stebutt's *Lehrbuch der allgemeinen Bodenkunde* (1930) is another excellent summary of Russian soil science, with emphasis on morphology, genesis, classification, and dynamics. Stebutt's book develops the concept of zonal, intrazonal, and azonal soils that has proved so useful to American soil scientists.

(7) Joffe's soil text, entitled *Pedology* (1936), is valuable, especially for its summaries of the Russian literature and for its discussion of soil phenomena in the tundra regions where sub-

soils are permanently fozen. There is much additional valuable material in the book. Many soil scientists disagree with some of Joffe's interpretations of soil descriptions taken from Federal-State soil survey reports. For example, we do not know any correlator who would classify Idaho's Portneuf silt loam as a Solonetz (p. 159). It is generally recognized to be a Sierozem, or light-gray zonal soil of the semi-desert. This kind of error emphasizes the need for standardization of soil terminology.

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